TRANSACTIONS

OF THE

ROYAL SOCIETY OF SOUTH AFRICA

VOLUME XIV.
1927.

WITH TWENTY-TWO PLATES, TWO MAPS, EIGHT CHARTS, AND TWO ILLUSTRATIONS OF ZAAMENKOMST SLAB.

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TRANSACTIONS

OF THE

ROYAL SOCIETY OF SOUTH AFRICA.

VOL. XIV.

ON INSTRUMENTS AND METHODS FOR STEREOSCOPIC SURVEYING.

By H. G. Fourcade.

(With Plates I–IV, and eleven Text-figures.)

CONTENTS.

Prefatory Note.

This paper, of which an abstract appeared in the British Association Report for 1905, was first written in that year, but its publication was deferred in the hope that an extended survey of a tract of country, making use of the stereoscopic method for the delineation of the topography, could have been provided for.

Owing, however, to the abandonment by the Cape Government, in 1904, consequent upon the long-continued financial depression in the Colony at that time, of the surveys on which the author was engaged, no further test of the method was found possible, and the subject was set aside.

The late war and recent developments having again brought photographic surveying to the fore, it is thought that many portions of the paper, notably the investigation of the distortion of a photographic lens over a wide field, which indicates the possibility of constructing a lens practically free from distortion, and the details of a machine for the stereoscopic measurement of points on photographic plates, which embodied carefully considered features, and probably remains the most accurate of its kind to-day, might still be of value. It was also thought that the investigation, having been concerned with a special machine and method, had best be left in its original form, reserving for later papers the extension of the method to air photography, a problem which received much attention from the author in 1903-4, and, being taken up by him again this year, was found to yield, it is believed, a satisfactory solution.

Introduction.

The instruments described in the present paper have been designed for the construction of topographical plans from stereoscopic photographs of landscape. Using an appropriate surveying camera, a photograph is taken from each end of a base line, at right angles to it, and under conditions ensuring accurate parallelism of the line of collimation of the camera in the two positions. The negatives or positives from them are then viewed in a stereoscopic measuring-machine, which, by combining the pictures, allows of the automatic identification of every corresponding pair of points on the plates. With the help of a micrometer in the machine and of a *réseau* scale impressed on the plates, the plate co-ordinates of any point may be measured. The three co-ordinates giving the position of the points on the ground may then be derived very simply from the measures and constants for the pair of plates, which are the focal length of the camera lens and the length of the base. When a sufficient number of points have been plotted from their co-ordinates, contour lines may be drawn.

A preliminary account of the method was given in a paper, "On a Stereoscopic Method of Photographic Surveying," read on 2nd October 1901 before the South African Philosophical Society (Trans. S.A. Phil. Soc., vol. xiv, pt. i, 1903; also Nature, 5th June 1902). Dr. C. Pulfrich, of Jena at nearly the same time and independently, devised a similar method, described in a paper, "Ueber neuere Anwendungen der Stereoskopie und über einen hierfür bestimmten Stereo-Komparator" (Zeitschrift für

Instrumentenkunden, March, May, and August 1902). Other references to stereoscopic surveying are contained in the following papers :—

H. H. Turner, "On a Simple Method of Accurate Surveying with an ordinary Camera" (Monthly Notices, R.A.S., lxii, No. 2, December 1901).

H. G. Fourcade, "Note on Professor Turner's recent Paper on Photographic Surveying" (Monthly Notices, R.A.S., lxii, No. 5, March 1902).

C. Deville, "On the Use of Wheatstone's Stereoscope in Photographic Surveying" (Transactions Roy. Soc. Canada, 1902–3, p. 63, May 1902).

C. Pulfrich, "Über die Konstruction von Höhenkurven und Plänen auf Grund stereo-photogrammetrischer Messunger mit Hülfe des Stereo-Komparators (Zeitschrift für Instrumentenkunden, Feb. 1903).

C. Pulfrich, "Über eine neue Art der Herstellung topographischer Karten und über einen hierfür bestimmten Stereo-Planigraphen (Zeitsch. f. Instr., May 1903).

C. Pulfrich, "Über einen Versuch zur praktischen Erprobung der Stereo-Photogrammetrie für die Zwecke der Topographie" (Zeitsch. f. Intr., Nov. 1903).

C. Pulfrich, "Über die Anwendung des Stereo-Komparators für die Zwecke der topographischen Punktbestimmung" (Zeitsch. f. Instr., Feb. 1904).

C. Pulfrich, "Über die Nützbarmachung des Stereo-Komparators für den Monokularen Gebrauch und über ein hierfür bestimmen monokulares Vergleichs-Mikroskop" (Zeitschr. f. Instr., June 1904).

A. Laussedat, "De l'emploi du stéréoscope en topographie et en astronomie" (Comptes rendus, 136, p. 22, 1903).

A. Laussedat, "Sur l'emploi d'images stéréoscopiques dans la construction des plans topographiques" (Comptes rendus, 138, p. 1039, 1904).

A. Laussedat, "Sur différents résultats récemment obtenus par la métrophotographie" (Comptes rendus, 139, p. 391, 1904).

A. Laussedat, "La Stéréoscopie appliquée à la constructions des plans" (Recherches sur les instruments, les méthodes et le dessin topographiques, Chap. iv, Annales du Conservatoire des Arts et Métiers, 3[ième] Série, t. iv, 1903).

A. von Hübl, "Die stereophotogrammetrische Terrain-Aufnahme," Wien, 1904 ; Verlag der K. u. K. militär-geographischen Institutes.

The stereoscopic method of surveying was occasionally used by me, in an elementary form, since 1898, to analyse distant and badly defined topography, which was then interpolated by sketching in between known points of the picture. The remarkable help which this simple artifice gave led me to attempt the measure in three dimensions of the stereoscopic image.* After devising direct mechanical methods of tracing the contour lines and

* See "The Observatory," June 1902, p. 238.

rejecting these provisionally as wanting in accuracy,* the Repsold machine used at the Cape Observatory for the measurement of astrographic plates was examined in 1901, through the courtesy of Sir David Gill, and the leading features of that admirable instrument † were copied in a form adapted to stereoscopic use. Several excellent ideas were also taken from the description of the Cambridge measuring-machine,‡ which later I had the advantage of being shown by Mr. A. R. Hinks. At Dr. Pulfrich's invitation, I also examined and tested in 1903 his "Stereo-Comparator," and I am indebted to Dr. Pulfrich and Dr. Loewe for much attention in supervising the construction at the Zeiss optical works of the optical parts of my own instruments and of the delicate glass scales of the micrometers. The mechanical parts were constructed by Messrs. Troughton & Simms in 1903, and the division of the réseau scale was made by M. Gautier. These firms spared no pains in endeavouring to satisfy the somewhat exacting requirements that seemed to me necessary to attain the accuracy aimed at, and it is satisfactory to find that the tests to which the instruments have now been subjected indicate workmanship of the highest order in all the essential parts.

The cost of construction of the instruments has been defrayed, in part, from a grant for the purpose made by the Prime Minister of Cape Colony in April 1902, at the initiative of the Council of the S.A. Philosophical Society (Proceedings S.A. Phil. Soc., 1901–2, p. xxvi, Nov. 1901).

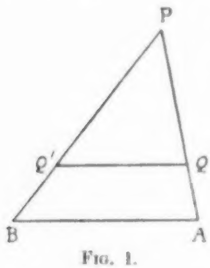

Fig. 1.

Theory of the Method.§

Let A and B (fig. 1) be the ends of the base, and Q and Q′ the positions on the photographs of any point P.

Take A as origin and AB as positive direction of, x-axis.

Let (X, Y, Z) be the co-ordinates of P: (x_a, f, z_a) (x_b, f, z_b) the co-ordinates of Q and Q′.

The equation of AP is

$$\frac{x}{X}=\frac{y}{Y}=\frac{z}{Z}$$

and if we put $y=f$, we get

* The chief reason was that until a lens practically free from distortion is produced, no mechanical method can possibly vie in accuracy with that of computation by points.

† Monthly Notices, R.A.S., lix, No. 2, Dec. 1898.

‡ Monthly Notices, R.A.S., lxi, No. 7, May 1901.

§ Extracted from the previous paper in Trans. S.A. Phil. Soc., xiv, pt. 1.

$$x_a = \frac{f}{Y}X,$$

$$z_a = \frac{f}{Y}Z.$$

Similarly the equation of BP is

$$\frac{x-b}{X-b} = \frac{y}{Y} = \frac{z-h}{Z-h},$$

where b and h are the x and z co-ordinates of B.

Whence

$$x_b = \frac{f}{Y}(X-b)+b,$$

$$z_b = \frac{f}{Y}(Z-h)+h.$$

From these equations we find

$$x_a - x_b + b = \frac{bf}{Y} = e.$$

e is the *stereoscopic difference*, constant for points in any plane perpendicular to Ay and vanishing for points at infinity.

The values of the co-ordinates of P follow

$$Y = \frac{b}{e}f,$$

$$X = \frac{b}{e}x_a,$$

$$Z = \frac{b}{e}z_a.$$

A check is afforded by the values of X and Z derived from BP.

$$X = \frac{b}{e}x'_b - b,$$

$$Z = \frac{b}{e}z'_b - h,$$

x'_b and z'_b denoting here the co-ordinates of Q′ referred to B.

The measurement of the co-ordinates of a point being made independently on each plate, although simultaneously, it will be a sufficient condition for the viewing apparatus to make corresponding portions of the two pictures combine with or without change of perspective.

Using a magnifying optical system to view the pair of plates, the condition for distinct vision is that the two images of any point appear in a *corresponding plane of vision*, so that the visual rays meet in space. This

condition evidently remains satisfied when the images are magnified, or when they are brought nearer together along a line parallel to that joining the nodal points of the two eyes, and for different distances between the viewing lenses or the eyes, since in all these cases the lines joining the two images of a point remain parallel to the eyes.*

The Surveying Camera and its Use.

The camera (Plate I, fig. 1) consists essentially of a metal box provided with levels, a transverse telescope, and a *réseau* scale, which may be set in front of the sensitive film for the impression of the réseau lines or removed for the exposure of the view. It is oriented and levelled by means of a vertical axis and three footscrews. A rising front carrying the lens serves to displace the horizon line, but normally it is kept clamped at the zero of its scale. A short cross-slide allows of lateral adjustment of the lens. Light extraneous to the picture is cut off by a shade with a suitable rectangular aperture.

The réseau, consisting of a scale of cross-lines 5 mm. apart was divided most accurately by M. Gautier on the silvered back surface of an optically plane and parallel plate of glass about 5 mm. in thickness, which then received a coating of amber varnish to protect the delicate ruling. The réseau plate is held in a metal frame by a "geometrical clamp," with six stops opposed by springs. This frame is hinged at its foot by means of a horizontal axis resting in segmental bearings. One rounded end of the axis is pressed against a small hardened and polished vertical plate by a spring acting at the opposite end, so that the réseau plate may be let down or set up again without disturbing its correct register in the camera. A double arm, connected with the frame by a forked piece, serves to raise or lower the réseau from outside the camera without introducing unnecessary constraints.

In its vertical position the réseau frame butts against a stop in the

* The geometrical theories of the stereoscopic image and of binocular vision were first given by Helmholtz in his "Handbuch der Physiologischen Optik," which is the "Principia" of the subject and implicitly anticipates much of the later more prolix work. A lucid account of these theories may be found in Heath's "Geometrical Optics," the treatment and notation being practically the same as in the present paper. Following Helmholtz (*loc. cit.*, Zweite Auflage, 1896, p. 812) and later optical writers, I made use in my 1901 paper of the term "stereoscopic difference" to denote the difference in the co-ordinates of a point on two plates in stereoscopic perspective. Some recent writers on stereoscopic measurement, apparently unacquainted with Helmholtz's classical work (see Zeitsch f. Instr., May 1903, p. 133, footnote, for one instance), use the word "parallax" in the same sense, but the change seems to me unwarranted and confusing, a parallax being essentially an angle, and a stereoscopic difference essentially a length.

camera box, and may then be locked by means of two projections on a horizontal rod turned by a worm gear, the pressure being regulated by a spring on the frame. When the réseau plate is let down, it is covered and locked by a metal plate worked by an outside arm near the front of the box. This serves also to prevent reflections from the back surface of the réseau during the exposure of the plate.

The réseau is impressed upon the sensitive film by light reflected through the lens from a white surface held in front of the latter. The réseau plate does not quite touch the film, a clearance of about 0·5 mm. being left, so that the réseau can be set up or let down without disturbing the plate or vice versa. The image of the réseau being projected from the lens, ordinary commercial plates with sensible curvatures may be used without detriment to accuracy, since any resulting distortion in the picture is reproduced in the réseau, and differentially eliminated in measures for which the réseau supplies the scale. To avoid the inconvenience which varying sizes of réseau intervals would occasion, the plate is placed in the measuring-machine at a distance from the microscope objective equal to the focal length of the camera lens and with the film in the same relative position, so that runs remain practically constant.

The width of cut of the réseau lines was made about 0·02 mm. to minimise the effect of diffraction on their definition on the plate at a distance of 0·5 mm.* The result is very satisfactory.

The size of plate adopted is $101{\cdot}5 \times 127$ mm. (4×5 inches). The plate is pressed during exposure by springs in the exposing slide against three stops in the camera. Each plate is carried in a metal sheath cut away at three places corresponding to the stops in the camera and to opposite studs in the exposing slide. Therefore no bending of the plate can result from its setting for exposure.

The exposing slide consists of a wooden box containing a set of springs, against which a board may be screwed back or moved forward by turning a nut at the back. It is loaded by dropping into it a plate from a changing box (shown in fig. 2, Plate III) holding twelve. By turning a small lever actuating an eccentric, a flat spring in the side of the slide is released and made to clip the plate, while the changing box and the slide are inverted together to allow the remaining plates to drop back into the changing box and the respective shutters to be replaced. The slide may now be placed in the camera, the shutter drawn, and the plate moved forward up to the stops by turning the back nut which releases gradually the spring board in the slide. After exposure the plate is drawn back into the slide and dropped into the back of the changing box, which is provided with a shutter on either side.

* A. R. Hinks, Monthly Notices, R.A.S., lix, June 1899, p. 530.

The lens adopted is Zeiss' "Protar," Series V, No. 3, an unsymmetrical doublet of f/18 aperture and 141 mm. nominal focal length.*

The mounting was specially made of only two parts, one of the lenses being alone removable. A stop of f/36 is used for all the exposures.† The lens may thus be left permanently fixed to the rising front, the outer surfaces remaining accessible for cleaning, and the inner forming part of a dust-tight cell which contains the diaphragm disk. This secures a constant adjustment of the optical axis of the lens with reference to the centre of the réseau. There is no provision for focussing. The principal focus was determined by Messrs. Zeiss with Abbe's focometer, as also the "extension" from the flange of the mount, and the camera built so as to bring the plate accurately into the plane of best definition for distant objects.

The exposures are made through a dark-yellow screen set in front of the lens. This screen was optically worked by Messrs. Zeiss to a departure from parallelism of under half a second.

The camera is constructed mainly of an aluminium alloy, and weighs with the changing box and a dozen plates only 14 lbs., so that it is sufficiently portable for mountain work.‡

Adjustments of the Camera.—Certain adjustments are left to the maker. The front slide is constructed to be parallel to the vertical réseau lines. The effect of any departure from parallelism may be eliminated by determining the origin of the réseau co-ordinates and the focal length for one upper and one lower reading of the front scale, and setting the slide to one of these readings whenever it becomes necessary to raise or lower the lens

* The radii r, thicknesses e, both in mm., and refractive indices n for the line D of the spectrum are as follows :—

Front Lens : I. $n=1{\cdot}55247$; $r_1=+13{\cdot}14$; $r_2=+\ 6{\cdot}61$; $e=1{\cdot}25$.
II. $n=1{\cdot}51720$; $r_3=+\ 6{\cdot}61$; $r_4=+14{\cdot}71$; $e=1{\cdot}76$.
Back lens : I. $n=1{\cdot}51674$; $r_5=-28{\cdot}33$; $r_6=+20{\cdot}13$; $e=1{\cdot}00$.
II. $n=1{\cdot}57360$; $r_7=+20{\cdot}13$; $r_8=-28{\cdot}33$; $e=2{\cdot}89$.

The axial distance between the lenses is 2·88 mm., and the diaphragm is midway.

† In a good lens the best definition is obtained with a stop of f/25 to f/30, beyond which the effect of diffraction tends to decrease the sharpness of the image. But, on the other hand, further stopping improves the images of points at near distances, for which the principal focus is retained and reduces distortion, so that a slightly smaller aperture such as f/36 will be about the most suitable for a camera with fixed focus.

‡ The camera was marked by the makers, 1904, but it was completed, as were the other instruments, in December 1903, when the author left England after having attended to their construction. The stereocomparator of Dr. Pulfrich was also completed in 1903, after an experimental model had been first made, but his surveying camera only a year or two later. In the latter instrument the shape of the body and the use of a transverse telescope follow the design in my 1901 paper. Dr. Pulfrich was averse to the use of a réseau, thinking that réseau lines would interfere with the image, but, as it turned out, the stereoscopic combination of the multitude of points which go to form the picture so overpowers the réseau lines that their presence does not cause the smallest inconvenience.

to take in the picture.* The vertical axis is also constructed sufficiently parallel to the vertical réseau lines, and the horizontal axis of the telescope sufficiently perpendicular to the plane of the réseau. The vertical axis is used merely to set the camera in azimuth, and any disturbance of the levels caused thereby may be easily rectified with the footscrews. And, as will be shown later, the method of setting the camera eliminates any error which might otherwise arise from a small inaccuracy in the position of the horizontal axis.

The conditions which remain to be satisfied by adjustment are:

(1) *Plane of réseau perpendicular to longitudinal level.*

(2) *Line of collimation of camera perpendicular to plane of réseau.*

(3) *Horizon line of réseau parallel to transverse level.*

(4) *Line of collimation of telescope perpendicular to line of collimation of camera.*

Adjustment (1) is effected with the help of an accurate level fitted with a reflecting eye-piece and set up in front of the camera after its line of collimation has been made truly horizontal by ordinary methods. (*a*) The camera lens being removed, the camera is levelled and oriented until the cross-wires of the level coincide with their image reflected from the front surface of the réseau. (*b*) The bubble of the longitudinal level is brought to the centre of its run by means of its adjusting screws, and the reading of the transverse level and the bisection of the telescope on a distant object noted. (*c*) The camera lens is replaced. With care this may be done without disturbing the camera, but if any slight displacement result it may be rectified by reproducing the bisection in the telescope and the level readings.

(2) The lens is next adjusted horizontally and vertically by means of the appropriate screws until the central intersection of the réseau lines, as seen through the lens, is bisected in the level telescope. The reading of the front scale is noted.

Adjustment (3) may now be effected by turning the footscrews until either end of the horizon line of the réseau, viewed through the lens, may be bisected by the cross-wires of the level when at the same time the longitudinal level of the camera is horizontal. The bubble of the transverse level may now be brought to the centre of its run by means of its adjusting screws.

(4) Two theodolites, A and B, are set up at the height of the camera lens C, and A collimated with C and B with the camera telescope D. Then (*a*) turn D 180° round its horizontal axis and change pivots. (*b*) Collimate C with B. (*c*) Adjust the difference in collimation between A and D, one

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half by turning A and the other half by moving the diaphragm of D. Repeat until the error becomes insensible. (*d*) Check by collimating A alternately with B and C, and B alternately with D and A, reading the circle each time. Measure again after changing faces of vertical circle. The means will give the two angles at A and B, and the angle between the two lines of collimation of the camera will be $180° - A - B$.

The bearings of the glass réseau plate, brass frame, and aluminium camera box are arranged to form a system compensated for temperature changes, as regards the "principal" line of the réseau.

Residual Errors of Adjustment of the Levels.—The correction $k \,.\, \Delta a$ to the readings of the longitudinal level may be computed from the plate co-ordinate x of a point near the middle vertical line of the plate, of which the angle of elevation a is also known. For then

$$\Delta a = \cos^2 a\left(\tan a - \frac{z}{\sqrt{x^2+f^2}}\right).$$

The correction $k\theta$ to the reading of the transverse level may also be found from the z co-ordinates of the same point on two plates exposed with different orientations. Then

$$\frac{z_2 - z_1}{x_2 - x_1} = -\tan\theta.$$

If the values of the level divisions have been determined with a level tester before the camera adjustments are made, the readings $-k \,.\, \Delta a$ and $-k\theta$, which will render horizontal the line of collimation of the camera and the horizon line of the réseau, may be derived at any time from the plate co-ordinates of a sufficient number of points and their observed angles of elevation. The camera may then be levelled to these readings, and corrections for level avoided without disturbing the original camera adjustments.

Stands.—Two similar stands form the ends of the base line. On either of these the camera, a signal, or a 5-inch micrometer theodolite, shown in fig 2, Plate I, may be interchanged. The theodolite serves to connect the ends of the base with the triangulation of the country.

The stands are "open framed." Each leg is hinged on the metal top by means of transverse rods ending in pivots supporting segmental bearings. Three small plates, which may be loosened by thumbscrews, serve to keep the pivots on their bearings when the stand is carried about, and allow of the legs being detached from the top and packed together in small compass if more convenient for transport. Warping of the woodwork is prevented by soaking the parts, before assembling together, in a bath of melted paraffin for two or three days. A similar theodolite stand has done good

service for some years and proved far superior in steadiness and freedom from "station-twist" to the much heavier stands, not geometrically conditioned, which are ordinarily used in geodetic work.

Signal.—The signal (shown in fig. 2, Plate III) consists of a plate with a rectangular aperture through which a mirror reflects zenithal light. This plate is hinged, at a height corresponding to the plane passing through the centres of the spherical ends of the footscrews of the instruments, to a cup fitting the central circular aperture of the top of the stand. A short cross-level serves to set the mark vertically over the hinge. For all moderate inclinations of the top of the stand, the centering of the signal will then correspond within a fraction of a millimetre to that of the vertical axis of a camera or theodolite resting on the three V-grooves.* Two such signals are provided in order to save the additional journey, between the two stations, that would otherwise be necessary.

Orientation of Camera.—At the second station the camera telescope is turned 180° round its horizontal axis and the pivots are changed. This eliminates in the stereoscopic difference the effect of inclination of the horizontal axis and of any small departure from 90° of the angle between the lines of collimation of the camera telescope and the camera. Any residual error in orientation would be due to error of bisection, imperfection of the pivots, or temperature distortions. A test of this method of preserving the parallelism of the camera in its two portions was made by collimating two telescopes, setting the camera betwen the pair, and adjusting the camera telescope on one of the collimators. After reversal of the camera telescope and change of pivots no appreciable error could be found in the adjustment on the second collimator.

It may be advisable, however, to observe at each station the angle between the base line and a number of well-defined points near the centre of the view. If from unequal heating or other cause there is found a small difference a between computed and observed angles, a correction may be applied to the plate, xs.

Let $$\theta=\tan^{-1}\frac{x}{f}.$$

When a is a small angle,

$$\begin{aligned}\Delta x&=-\frac{fa}{\cos^2\theta}\\&=-fa(1+\tan^2\theta)\\&=-fa\left(1+\frac{x^2}{f^2}\right).\end{aligned}$$

* With a moderate amount of care in setting up the stand, the difference in height of the levelling screws need not exceed 5 mm. Each screw being 71 mm. from the centre, the error in centering, due to inclination of the stand, will then be within 0·04 mm.

This correction would in general be so small that it could be applied sufficiently by tabulation for about 10 values of x, differing by 1 cm. near the centre of the plate and 0·5 cm. near the margin.

Length of Base.—The length of the base should not exceed one-seventh or one-eighth of the distance of the nearest objects which it is required to combine stereoscopically. Nearer points, admitting of separate identification on the pair of plates, may be measured independently on each. On the other hand, the length should not be less than will give the necessary accuracy for the greatest distances operated at. The table at p. 44, showing the errors in the co-ordinates for different distances and lengths of base, will allow of the choice of a suitable length.

Parallactic Measurement of the Base.—In many cases the most convenient method of determination of the length of the base with sufficient accuracy is by observation, from both ends, of three or more known points.

The co-ordinates of one end of the base are first computed by the three-point problem, or from all the angles observed if greater accuracy be needed.* With the resulting values of y and x the angles of direction and the distances of the observed points are computed. From each triangle joining the base with an observed point a value for the base may now be derived:

$$b = \frac{a \sin (A + B)}{\sin A},$$

the weighted mean of which is adopted.

* In this case let (y_1, x_1) be the approximate values obtained from the three-point solution. The "angles of direction" between (y_1, x_1) and each of the points observed are computed, as also their changes α and β for a change of $+1$ in y_1 and x_1. Let A_1 be an angle of direction, and Y_1, X_1 the corresponding x- and y-distances. Then

$$\alpha = -\frac{\cos^2 A_1}{X_1 \sin 1''}, \qquad \beta = \frac{\sin^2 A_1}{Y_1 \sin 1''},$$

and the corrected angles of direction are

$$A_1 + \alpha_1 \Delta y + \beta_1 \Delta x.$$
$$A_2 + \alpha_2 \Delta y + \beta_2 \Delta x.$$
$$\cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot$$

Let C_1 be the computed value, $A_2 - A_1$, of the observed angle O_1 and put $C_1 - O_1 = l_1$. We may form observation equations of the type

$$(\alpha_2 - \alpha_1)\Delta y + (\beta_2 - \beta_1)\Delta x + l_1 = v_1,$$

which lead to two normal equations in Δy and Δx.

This method is not used in ordinary surveying as much as it should be, the arithmetical work being light and the solution rigorous. It is very valuable for determining accurately and with minimum labour the position of an additional point after a triangulation has been completed.

The error in the determination of the position of the base may be regarded as negligible in comparison with that in its length. Then

$$db = \frac{a \cos (A+B)}{\sin A} dB - \frac{a \sin B}{\sin^2 A} dA.$$

With sufficient approximation we may take $A+B=180°$ and $A=B$. We get

$$db = \frac{a}{\sin A}(dB - dA).$$

If ϵ_b and ϵ be respectively the probable errors in the base and in an observed angle,

$$\epsilon_b = \frac{a\sqrt{2}}{\sin A}\epsilon,$$

or

$$\frac{\epsilon_b}{b} = \frac{\sqrt{2}}{p}\epsilon,$$

where p is the parallax $(180° - A - B)$.

Take $a = 10b$, $A = 45°$. Then

$$\frac{\epsilon_b}{b} = 20\epsilon.$$

If $\epsilon = \pm 1''$ and the weighted mean from four triangles is used, the probable error of the base will be

$$\frac{\epsilon_b}{b} = 10\epsilon = \frac{1}{21800}.$$

In the base determined in this manner for the first field trial of the stereoscopic method the agreement of the values derived from different known points was within $\frac{1}{100000}$.

The measurement of the small angles at the distant points would greatly augment the labour of the operation without commensurate increase in the accuracy of the result. In small triangles the principal errors are made in centering the instrument and the signals. At the base ends these errors are avoided by making use of a theodolite and a signal interchangeable on the same stand and mechanically centered to within 1 mm. Small errors in the stations observed or in their known positions affect the measures at both ends of the base almost equally and are differentially eliminated in the results. But the angles subtended by the base at the surrounding stations could not be measured with equal accuracy because then the ends would no longer be marked by the stands but by ordinary signals. With a 5-inch micrometer theodolite and two arcs the parallaxes may be measured with

a probable error not exceeding one or two seconds if the precaution be taken of using parallel settings of the circle at both sections, whereby the systematic error of graduation not eliminated in the mean of two arcs is largely reduced differentially. The distances being small, lateral refraction is not of serious import, and would also tend to be eliminated differentially.

The accuracy of ordinary chaining would as a rule be less than that of the parallactic method, and the latter has in rough ground the very great advantage of allowing a free choice of points of view which could not otherwise be adopted on account of the difficulty of measuring their distance apart. When photographing mountainous country from plains the direct measurement of the base with a steel tape may, however, become preferable.

Exposure of the Plates.—The plates used are Edward's medium isochromatic. Their sensitiveness when exposed behind the yellow screen is almost entirely limited to the region of the spectrum between wave-lengths 0·52 μ and 0·59 μ, with a maximum at 0·55 μ. Bouguer's law of absorption of radiation by the atmosphere may therefore be considered applicable to the light acting upon the plates, without any modification on account of the different transmissibility of rays of different wave-lengths. The intensity I of the light transmitted, in terms of the intensity when the sun is in the zenith, is then

$$I = p^{s-1},$$

s being the ratio of the path of the rays through the atmosphere to that of a vertical ray. With a suitable value of the transparency constant p, the formula may be made to include the intensity of light reflected by the sky.

Abney's observations on the transmission of sunlight through the earth's atmosphere yield a value of $p = 0{\cdot}83$ at sea-level and for wave-length 0·55 μ. For an altitude at which the barometric pressure is P,

$$\log p = \frac{P}{P_0} \log p_0.$$

This would make $p = 0{\cdot}88$ at 3000 m. altitude, but Abney's results give 0·91, a difference consistent with the greater dryness and purity of the air at high elevations. These values of p, being for the very clearest weather, are subject to large reductions in other states of the atmosphere. On fine days, however, and when the sun is not too low, they will be found sufficiently accurate for the purpose of estimating the exposure.

A table was computed, for latitude 35° S., of the altitude of the sun for each hour of one day in every month. The corresponding intensity of light was then derived for $p = 0{\cdot}83$ and $p = 0{\cdot}91$ and corrected for the relative

square of the sun's diameter. The resulting comparative exposures are given in Tables I and II, the unit being the exposure at sea-level with the sun in the zenith.

TABLE I.—*Comparative Exposures for Latitude 35° S. and Sea-level.*

	Apparent noon.	A.M. 11. P.M. 1.	10. 2.	9. 3.	8. 4	7. 5.	6. 6.
Jan. 1	0·97	0·98	0·99	1·03	1·10	1·25	1·83
Feb. 1	0·99	0·99	1·01	1·05	1·13	1·34	2·37
Mar. 1	1·01	1·02	1·04	1·09	1·21	1·55	
Apr. 1	1·06	1·07	1·10	1·18	1·39	2·47	
May 1	1·13	1·15	1·20	1·34	1·81		
June 1	1·21	1·23	1·31	1·53	2·60		
July 1	1·22	1·23	1·33	1·56	2·85		
Aug. 1	1·17	1·20	1·25	1·42	2·07		
Sept. 1	1·09	1·11	1·14	1·24	1·50	3·18	
Oct. 1	1·04	1·05	1·07	1·13	1·27	1·77	
Nov. 1	1·00	1·01	1·03	1·07	1·16	1·39	2·89
Dec. 1	0·98	0·99	1·00	1·04	1·12	1·26	1·94

TABLE II.—*Differences for 3000 m. (10,000 ft.).*

	Apparent noon.	A.M. 11. P.M. 1.	10. 2.	9. 3.	8. 4.	7. 5.	6. 6.
Jan. 1	0·08	0·09	0·10	0·12	0·16	0·25	0·61
Feb. 1	0·09	0·09	0·10	0·13	0·17	0·30	0·97
Mar. 1	0·10	0·10	0·11	0·14	0·21	0·41	
Apr. 1	0·12	0·12	0·14	0·18	0·31	1·01	
May 1	0·15	0·16	0·19	0·28	0·57		
June 1	0·19	0·20	0·25	0·38	1·08		
July 1	0·19	0·20	0·26	0·40	1·26		
Aug. 1	0·17	0·18	0·21	0·32	0·73		
Sept. 1	0·13	0·14	0·15	0·21	0·36	1·50	
Oct. 1	0·11	0·11	0·12	0·16	0·24	0·54	
Nov. 1	0·09	0·10	0·11	0·13	0·18	0·32	1·30
Dec. 1	0·09	0·09	0·10	0·12	0·17	0·24	0·69

To use the table, trial exposures are first made until found correct for a certain day and hour and light. Suppose, for instance, that at 3 p.m. on Sept. 1, with a bright day and operating at an altitude of 1000 feet, a correct exposure is found to be 10 seconds, it is seen by reference to the

table that the unit exposure is $\frac{10}{1{\cdot}24-0{\cdot}02}=8$ seconds. This, multiplied by the number in Table I, decreased by a proportional part for altitude derived from Table II, will give the exposure for other days and hours and altitudes. The result requires to be further multiplied by a factor varying from 1 on a normal bright day, or 2 with a faint sun, to 8 on a very dull, cloudy day, and will in any case apply only to the class of subject—namely, distant landscape—for which the trial exposures were made.

The exposure for the réseau should be about twice that for the view, and to secure more even lines it is best given first. It is made by raising the réseau plate and holding in front of the lens a piece of white paper illuminated by skylight.

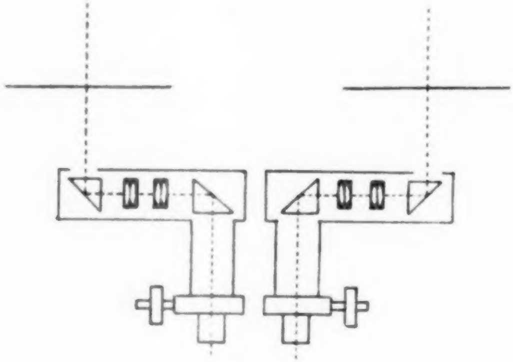

FIG. 2.

It will be noticed that the increase in exposure with zenith distance is much less than is required when using ordinary photographic plates, sensitive to rays for which p is smaller. For this reason the indications given by ordinary actinometers are not applicable.

Measuring Stereoscope.—The essentials (fig. 2) consist of a pair of micrometer microscopes adjustable to the width of the eyes of the observer, four prisms of total reflection introduced in the optical system to separate the plates a sufficient distance, and a mechanical stage on which the plates may be rotated separately, or set at different relative distances and heights, or moved together either horizontally or vertically.

The general construction of the machine is shown by figs. 1 and 2 (Plate II) and fig. 1 (Plate III). The base is of cast iron, cast in one piece with the pillar and the desk-like plate carrying the micrometer microscopes. The stage is inclined at an angle of 45°, and moves on cross-slides actuated by

the handwheels *b* and *h* (fig. 3). The guiding surfaces of each slide consist of a cylinder and plane, the guided part having four segmental bearings against the cylinder and one flat bearing against the plane. The cylinder is so placed as to bear a greater proportion, than the plane, of the weight of the supported parts. Thus, in the vertical slide, it is placed midway between the plates, and in the horizontal slide below the plane guide instead of above as in other measuring-machines. Each motion is

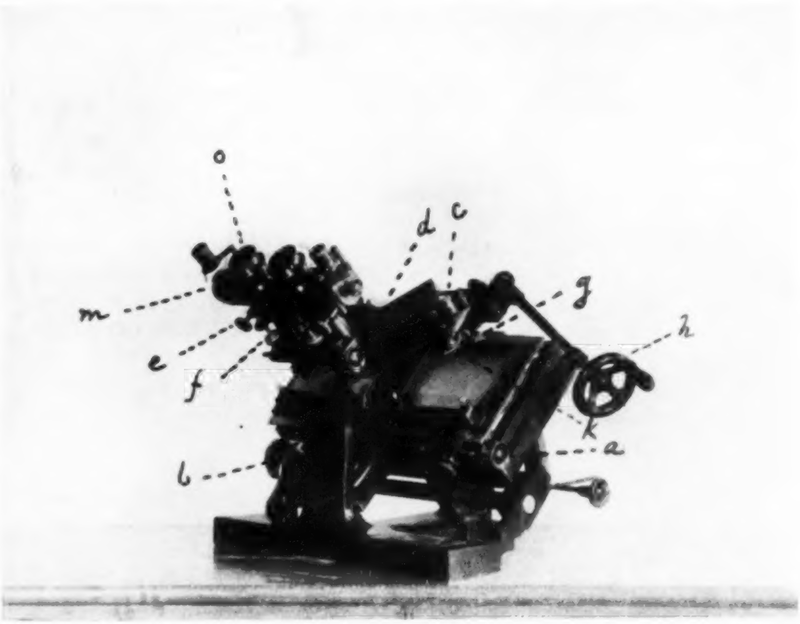

Fig. 3.

transmitted by a screw, of which the axis is so placed that it coincides, as nearly as is practicable, with the resultant of the frictional resistances of the slide. Both nuts are tapped in the side of the moved frame farthest from the bearing-collar, so that, with very slight lateral play of the screw in its nut and bearing-collar, the frame bears quite freely on its proper guiding surfaces. Back-lash is prevented, in the horizontal screw, by a spring nut and collar, and in the vertical screw by the weight of the supported part. These arrangements make the slides "well conditioned," and their motion exceedingly smooth and true.

The plates are set side by side (fig. 4) at an inclination corresponding to

that of the base line, and at relative heights such that corresponding réseau points are at the same level. Their horizontal separation may be altered by means of the slow-motion screw *a* and the distance rod against which it acts. These move the right plate alone, while the left plate alone may be moved vertically by turning the screw *b*. The subsidiary slides giving these small ranges of horizontal and vertical motions are, like the main slides, "geometrical."

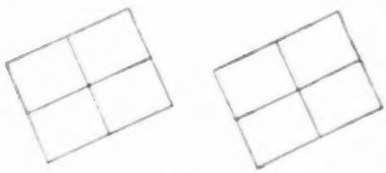

FIG. 4.

Each plate is pressed upwards, by springs, against the rounded ends of three screws, *g*, which agree in position with the three stops in the camera, and may be adjusted to remain in one plane when the slides are moved. This adjustment is effected by turning the screws until the apparent side of a réseau square remains the same at the ends of both the horizontal and the vertical diameters of the plate, or more conveniently with a micrometer depth gauge and a plate-glass plate. The holder carrying these screws is mounted on a graduated setting circle, held friction-tight in its frame by a circular corrugated spring. To insert a plate, the plate springs are depressed together by a light frame provided with projections for the fingers. When this frame is released it touches and presses the plate at only three points opposed to the screws, so that no bending of the glass can take place.

Each microscope tube is mounted on a box containing the prisms and the lens. This box may be rotated round the collar *k*, and bears upon the supporting plate at two other points, one of the bearings being on a projecting arm cast in one piece with the box. Since the microscopes are eccentrically mounted on the boxes, their distance apart may, by rotation of the boxes, be varied to suit the eyes of the observer. The motion is regulated by the screw *d* and measured by a small scale parallel to its axis. The boxes may then be clamped to their base plate by screws passing through slots in the latter.

The lens and prisms are mounted on a plate which may be slipped out of its box by loosening three screws. They are then accessible for cleaning without disturbing their adjustment. The lens is a symmetrical doublet of 20 mm. aperture and 70 mm. focal length, of special design, giving very fine definition over the whole of the visual field. It is mounted, midway between the micrometer and the negative, on a geometrical slide to which the screw *c*, with graduated head, gives a small range of motion. This arrangement has several important advantages: (1) As in the Cape and Cambridge machines, runs may be adjusted for without disturbing the

focussing. (2) The magnification being unity, and the optical system symmetrical, there is no appreciable distortion in the field. (3) The distance of the objective from the plates being the same as the focal length of the camera lens, runs remain practically constant, notwithstanding the variation in actual size of the réseau squares, which results from the central projection of the réseau upon a commercial plate having always more or less curvature.

The eye-pieces ordinarily used are Zeiss' "Orthoscopic," of 20 mm. focus and an angular field of about 40°. The focal length of the camera lens being 140 mm. and the magnification of the microscope objectives unity, the ultimate magnification of the landscape is $F/f = \frac{140}{20} = 7$. Similar eye-pieces of 30 mm. focus are also provided.

The plates are illuminated by light reflected by a pair of plane mirrors

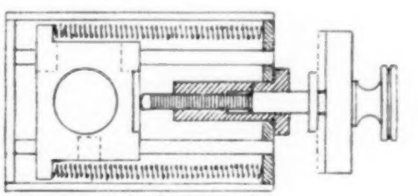

FIG. 5.

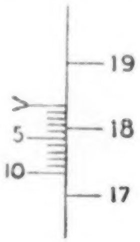

FIG. 6.

mounted on a rod near the base of the instrument and diffused by sheets of ground glass borne by the stage at about 1 cm. below the plates.

The construction of the micrometers is represented by fig. 5. The principle adopted is that of the Cambridge machine, in which a glass scale is moved by a micrometer screw. The slide is formed of two parallel steel rods, on which a plate carrying the glass scale rests at 3 bearings. One of the rods has two plane faces and fits a fork of the plate. The other rod is cylindrical, and passes through two accurately fitting holes in the plate. Spiral springs in tension keep the plate in contact with the rounded point of the screw. The plate and springs being clear of the micrometer box, friction is reduced to a minimum.

The screw is of half-millimetre pitch, and its head is divided into 50 parts. A small index scale (fig. 6) serves to subdivide each interval into tenths, so that with the aid of a lens of short focus readings may be made by estimation to 0·1 μ. The lens at the same time makes the reading very convenient by bringing the micrometer head into distinct vision from the level of the eye-piece.

The nut of the screw being fixed to the side of the micrometer box, the distance of the head from the box is variable. The index scale has then to be carried by the micrometer head, but it is prevented from rotating with the latter by an arm sliding out of a stop fixed to the micrometer box. On this stop is a scale of half-millimetres, recording the revolutions of the screw, but not usually read because a fraction of a revolution is sufficient for the measures.

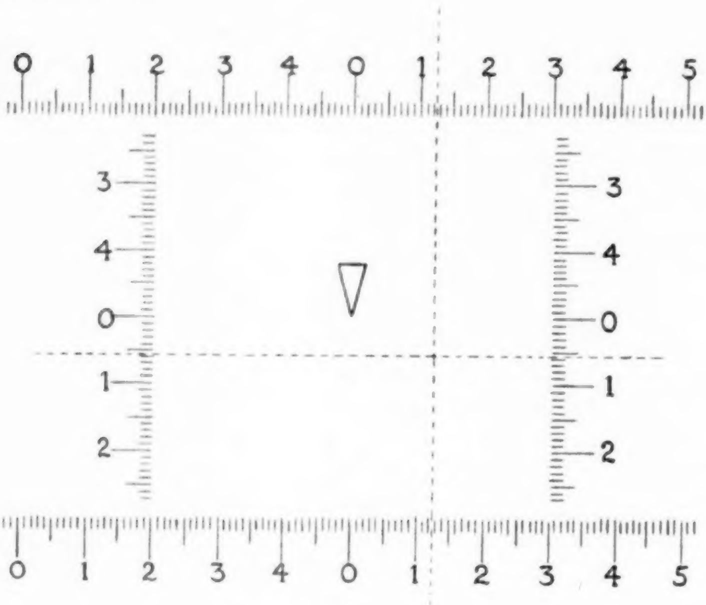

Fig. 7.

Fig. 7 represents the division of the glass scale. Two scales crossed at right angles would interfere with the stereoscopic bisection of the points observed. A square of scales is therefore employed. The index is at the intersection of the zeros of the scales. It is evident that mean readings of either pair of parallel scales will not be affected by any small error in the setting of the scales perpendicularly to the réseau lines.

The tubes carrying the micrometers rest in segmental bearings of the outer tubes. Focussing is effected, separately for each tube, by means of screws, *f*, with graduated heads. Several readings are taken, and the screw set as a permanent adjustment to their mean. The rotation of the tubes, when setting the micrometers to the inclination of the réseau lines,

is regulated by clamping collars and slow-motion screws. Fig. 8 shows the principle. $b_{1,2}$ and $b_{3,4}$ are the four segmental bearings of the outer tube, s_1 the focussing screw giving longitudinal motion, and s_2 the setting screw for position angle. s_1 and s_2 are both carried by the rotating clamping collar. The opposing stops have plane faces sufficiently wide to admit of the range of motion of the tube. The micrometer box not being symmetrically disposed about the tube, its weight and that of the tube are sufficient to maintain the six contacts which determine the position of the tube. But to prevent accidental disturbance during measurements the inner tubes, which are of thick gun-metal and accurately turned, may be clamped against the bearings $b_{1,2}$ and $b_{3,4}$, once the adjustments have been completed.

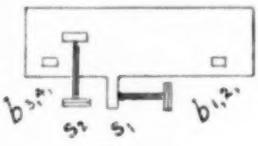

Fig. 8.

The setting scales on the main slides are divided, on ivory, into 5-mm. intervals. The lower scale, a (fig. 9), is borne by the plate-holder and remains parallel to the horizontal R-lines when the plate is rotated. The upper scale is attached to a collar, the axis of which coincides with the axis of the microscope, and may be turned until it is parallel with the vertical R-lines and perpendicular to the lower scale. The upper scale is clear of the lower one, but the resulting parallax is too small to cause any difficulty in the counting of the R-intervals by reading the scales at their intersection. To avoid introducing plate co-ordinates of minus sign, those of the centre of the plate are made 10, 10 cm.

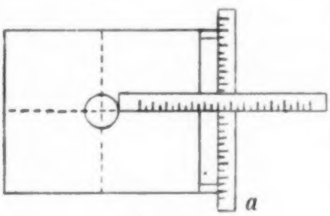

Fig. 9.

A pair of plates being placed in the machine and adjustment for focus made, each holder is rotated until both ends of the horizon line of the corresponding plate remains bisected by the index of the micrometer when the horizontal slide is moved. The verniers of the graduated circles are then read, and to these readings are added the inclination of the base line, constituting the settings for inclination. The micrometers are next rotated until the horizon lines of the plates are parallel with the lines joining the corresponding zeros of the glass scales. The index of the right micrometer being made to coincide with the intersection of the middle R-lines of its plate, the plate under the left micrometer is then moved vertically by the auxiliary slide until its central R-intersection also coincides with its micrometer index, both micrometers having been previously set to zero.

The next step is to adjust runs. The screws moving the microscope

objectives being provided with graduated heads, a number of readings may be taken of the settings which make the runs zero along the horizon line and the screws set at the mean. Or, if the value of a screw revolution has been determined, the runs may be measured with the eye-piece micrometers and the settings of the objective screws altered accordingly. The error resulting from further neglect of runs will as a rule be less than that which would remain if corrections were applied, in the ordinary way, to the mean of the measures of two R-lines. For in the one case the actual error due to errors in the impressed images of the réseau lines will be

$$e_1+k\frac{\Sigma e}{n},$$

and in the other

$$\frac{e_1+e_2}{2}-k(e_1-e_2)+\frac{e_1-e_2}{2}=e_1-k(e_1-e_2).$$

This is, however, assuming that the runs remain constant over the plate. When the inclination of the base line is considerable, the rotation of the plate to that inclination may alter slightly the plane of the plate which was adjusted for a horizontal setting. It would then become preferable to restrict the use of a mean run to limited regions of the plate, resetting for runs when the error would exceed $1\,\mu$, or whatever limit is fixed upon.

The measurements may then proceed as follows:—

(*a*) The micrometers are set to their zeros.

(*b*) The point to be measured is brought under the index of the left micrometer by moving the slides of the machine with the hand wheels. The right-hand plate is then moved in a horizontal direction by the screw of the auxiliary horizontal slide until the corresponding point on the right plate coincides with the right index. These bisections are made stereoscopically—that is, the picture appears in relief, and the indices of the two micrometers also combining appear as a single mark moving to and from the observer.

(*c*) With each micrometer the back division of the glass scale next to the vertical réseau line is made to bisect this line. Separate settings may be made for the upper and the lower scales, and the mean estimated at sight, or a mean bisection for the upper and lower scales directly made.

(*d*) For each micrometer the various scales are then read, giving all the figures of the measurement consecutively. First, the outer centimetre scale; then the glass scale, which gives the millimetres and tenths; and, finally, the micrometer head, which gives hundredths, thousandths, and, by estimation, ten-thousands of a millimetre, corresponding to less than one second of arc.

(*e*) The vertical scales are similarly read, the glass scales giving the millimetres and tenths, and by estimation hundredths, corresponding to 20 seconds of arc in the vertical angles, an accuracy which is sufficient relatively to that of distances derived from small stereoscopic differences.

The speed of the complete measurements, including all settings and readings of the pair of micrometers, was found to be, without practice, about 25 points per hour.

Comparison of Screws and Scales.

Division Errors of the Scales and progressive Errors of the Screws.—The progressive errors of each screw, the division errors of its scale, and the ratio of the screw to the scale were determined together by comparing each of 10 revolutions of the screw with every scale interval of 0·5 mm. A pair of parallel wires, about 0·05 mm. apart, was mounted on a diaphragm borne by the stage and the lines of the scale brought successively midway between the wires, in each of the 19 series giving all the possible combinations of the screw and scale intervals. A complete measure included the reading of the micrometer for corresponding upper and lower scale divisions, once in a forward and once in a reverse direction of the series. A simple method of reduction follows: If the measures are tabulated in vertical columns and horizontal rows corresponding to screw revolutions and scale intervals, the means of the rows will give relative values of the scale intervals, and the means of the columns relative values of the screw revolutions. The ratio of the screw to the scale is derived from the mean of the scale intervals. It is noteworthy that the combination of a screw and a scale in a measuring instrument not only renders the measures practically independent of wear of the screw, but also allows of the use of a very convenient method of determination of the errors of the screw and scale, not affected by optical distortion of the field.

Let $x_0, x_1 \ldots y_0, y_1 \ldots$ be the respective corrections to the scale divisions and for progressive error of the screw. The observation equations are:

$$
\begin{aligned}
&x_0-x_1-y_0+y_1-l_{01}=v_{01},\\
&x_0-x_1-y_1+y_2-l_{02}=v_{02}.\\
&\quad\ldots\ldots\ldots\ldots\\
&x_0-x_1-y_{n-1}+y_n-l_{0n}=v_{0n},\\
&\qquad x_1-x_2-y_1+y_2-l_{12}=v_{12},\\
&\qquad x_1-x_2-y_2+y_3-l_{13}=v_{13},\\
&\qquad\quad\ldots\ldots\ldots\ldots\\
&\qquad x_1-x_2-y_0+y_1-l_{10}=v_{10};\\
&\qquad\quad\ldots\ldots\ldots\ldots
\end{aligned}
$$

and the normal equations:

$$x_0-x_1-\frac{\Sigma l_0}{n}-y_0+y_n=0,$$

$$-x_0+2x_1-x_2+\frac{\Sigma l_0}{n}-\frac{\Sigma l_1}{n}=0,$$

$$-x_1+2x_2-x_3+\frac{\Sigma l_1}{n}-\frac{\Sigma l_2}{n}=0,$$

$$\cdots\cdots\cdots\cdots$$

$$x_{n-1}-x_n-\frac{\Sigma l_n}{n}+y_0-y_n=0.$$

Adding these equations there results

$$0=0,$$

and therefore the unknowns cannot be found without some further relation connecting them. If we put $z_1=0-x_1$, $z_2=x_1-x_2$, etc., and make $z_1+z_2+\ldots+z_n=0$, and introduce a similar condition in respect of the y's—that is, take the corrections to be those to a mean screw and mean scale—the terminal errors x_0, x_n, y_0, y_n become zero, and the normal equations reduce to

$$z_1=\frac{\Sigma l_0}{n},$$

$$z_2-z_1=-\frac{\Sigma l_0}{n}+\frac{\Sigma l_1}{n}.$$

$$\cdots\cdots\cdots$$

We get then

$$z_1=\frac{\Sigma l_0}{n},$$

$$z_2=\frac{\Sigma l_1}{n}.$$

$$\cdots$$

The corrections $x_1, x_2, \ldots$ are given by

$$x_1=-z_1,$$

$$x_2=x_1-z_2,$$

$$x_3=x_2-z_3$$

$$\cdots\cdots$$

and similarly for the y corrections.

The reduction gave for the left micrometer :

Scale interval.	Correction in microns.	Screw revolution.	Correction in microns.
2·5—3·0	—0·60	1	—0·59
3·0—3·5	—0·26	2	—0·20
3·5—4·0	+0·13	3	—0·19
4·0—4·5	+0·34	4	—0·24
4·5—0	+0·02	5	—0·26
0—0·5	+0·06	6	+0·30
0·5—1·0	+0·19	7	—0·10
1·0—1·5	—0·04	8	+0·39
1·5—2·0	+0·06	9	+0·62
2·0—2·5	+0·10	10	+0·28

Mean ratio of screw to scale 1·00247 ± 0·00003.

The sum, without regard to sign of the residuals of the 100 observation equations is 40·46 μ. By Lüroth's formula the probable error of a single measure is

$$0{\cdot}8453 \frac{40{\cdot}46}{\sqrt{100(100-20)}} = \pm 0{\cdot}382\ \mu.$$

The p.e. of determination of a scale interval or screw revolution is then

$$\pm \frac{0{\cdot}382}{\sqrt{10}} = \pm 0{\cdot}12\ \mu,$$

and the p.e. of a single bisection with the micrometer (mean of back and forward, reading both scales),

$$\pm \frac{0{\cdot}382}{\sqrt{2}} = \pm 0{\cdot}27\ \mu.$$

For the right micrometer the results were :

Scale interval.	Correction in microns.	Screw revolution.	Correction in microns.
2·5—3·0	—0·04	1	+0·54
3·0—3·5	+0·18	2	+0·96
3·5—4·0	+0·49	3	+0·32
4·0—4·5	+0·49	4	+0·21
4·5—0	—0·14	5	+0·05
0—0·5	+0·33	6	—0·22
0·5—1·0	—0·24	7	—0·31
1·0—1·5	—0·18	8	—0·46
1·5—2·0	—0·92	9	—0·51
2·0—2·5	+0·04	10	—0·58

Mean ratio of screw to scale $1{\cdot}00184 \pm 0{\cdot}00003$.

The sum of the residuals is $40{\cdot}08\,\mu$, and the several probable errors remain the same as before.

The investigation of the division errors of the scales was not carried further because, for most purposes, it seems sufficient to treat these errors as accidental, and, whenever special accuracy is aimed at, the measure can be referred to one of the divisions which have been determined.

Periodic Errors of the Screws.—An examination for periodic error was next made. Corresponding fifths of a screw revolution were compared with each of the scale intervals between divisions 0 and 0·5, the measures being conveniently arranged in series and reduced in the same manner as before. The final results were for the left screw, in microns:

$$f(\phi) = -0{\cdot}325 + 0{\cdot}271 \cos \phi + 0{\cdot}003 \sin \phi \\ + 0{\cdot}054 \cos 2\phi - 0{\cdot}003 \sin 2\phi,$$

and for the right screw:

$$f(\phi) = +0{\cdot}017 + 0{\cdot}076 \cos \phi - 0{\cdot}238 \sin \phi \\ - 0{\cdot}093 \cos 2\phi - 0{\cdot}015 \sin 2\phi.$$

The largest coefficient of any periodic term amounts to only a two-thousandth part of a screw revolution.* The measures being made to the nearest micron, or five-hundredth part of a revolution, are not affected by periodic error. The screws may therefore be considered, as regards periodic and progressive errors, to be both very good and for their ordinary use practically perfect.

Index Error.—The réseau lines being referred to the scales but the point observed to the central index, the error of that index has to be determined. This was done by taking a number of micrometer readings of the upper and lower scales and of the index when bisecting the pair of wires used in the other determinations. To eliminate error which might be due to want of straightness of the wires, these were reversed during half the measures. The corrections found were:

For left micrometer, $-3{\cdot}50 \pm 0{\cdot}05\,\mu$,
For right micrometer, $+6{\cdot}80 \pm 0{\cdot}07\,\mu$.

Total Corrections.—The following tables include all the corrections applicable to the micrometer readings and may be used whenever special accuracy is called for.

* The constants make the correction zero for micrometer division 0.

TABLE OF CORRECTIONS. LEFT MICROMETER.

Scale division.	Correction for index and scale.	Corrections for periodic and progressive errors.		
		Microm. division.	R. R. 5·5–6·0.	R. R. 6·0–6·5.
	μ		μ	μ
2·5	−3·1	0	0·0	0·0
3·0	−3·7	50	+0·1	0·0
3·5	−4·0	100	0·0	−0·1
4·0	−3·9	150	0·0	−0·1
4·5	−3·5	200	+0·1	−0·1
0	−3·5	250	+0·2	0·0
0·5	−3·4	300	+0·4	+0·1
1·0	−3·2	350	+0·6	+0·4
1·5	−3·3	400	+0·9	+0·6
2·0	−3·2	450	+1·3	+1·2
2·5	−3·1	500	+1·5	+1·5

TABLE OF CORRECTIONS. RIGHT MICROMETER.

Scale division.	Correction for index and scale.	Corrections for periodic and progressive errors.		
		Microm. division.	R. R. 5·0–5·5.	R. R. 4·5–5·0.
	μ		μ	μ
2·5	+5·8	0	0·0	0·0
3·0	+5·8	50	0·0	0·0
3·5	+6·0	100	0·0	+0·1
4·0	+6·4	150	+0·1	+0·1
4·5	+6·9	200	+0·1	+0·1
0	+6·8	250	+0·2	+0·3
0·5	+7·1	300	+0·5	+0·6
1·0	+6·9	350	+0·8	+0·9
1·5	+6·7	400	+0·9	+1·0
2·0	+5·8	450	+0·8	+1·0
2·5	+5·8	500	+0·7	+0·9

In ordinary work, the nearest scale division being measured from, only a fifth part of the screw revolution, between division 0 and 100, is brought into operation. The periodic and progressive errors are therefore insensible. For the index and scale corrections, it is sufficient to use mean values of $-3{\cdot}5\ \mu$ for the left micrometer and $+6{\cdot}4\ \mu$ for the right. These

corrections might be automatically applied by fixing stops on the micrometer drums, to give zero settings freed from error.

Distortion of Film and Errors of Réseau.—Positives from two star plates exposed under identical conditions (kindly communicated by Mr. S. S. Hough) were first compared. The direct measurement in the stereoscopic machine of the differences between corresponding distances of five pairs of stars gave (from the means of 10 observations, and both forward and back readings):

Stars.	Plate A—Plate B.	
	μ	
4–5	$-0{\cdot}19$	$\pm 0{\cdot}54$
11–12	$+5{\cdot}12$	$\pm 0{\cdot}33$
19–21	$+2{\cdot}30$	$\pm 0{\cdot}54$
42–41	$-6{\cdot}35$	$\pm 0{\cdot}57$
50–51	$-1{\cdot}54$	$\pm 0{\cdot}57$
Mean	$-0{\cdot}13$	

The sum of the squares of the departures from the mean is 74·14. If we regard the errors as accidental, the p.e. of the difference in distance of a pair of stars is:

$$\pm 0{\cdot}6745\sqrt{\frac{74{\cdot}14}{4}} = \pm 2{\cdot}90\ \mu \pm 0{\cdot}52.$$

Of this, the p.e. due to distortion of the film (including error inherent to the photographic image) will be:

$$\pm\sqrt{(2{\cdot}90)^2-(0{\cdot}52)^2} = \pm 2{\cdot}85\ \mu,$$

or, for a distance on either plate,

$$\pm\frac{2{\cdot}85}{\sqrt{2}} = \pm 2{\cdot}02\ \mu.$$

Since positives were examined, the errors include those of reproduction. For a negative the p.e. due to distortion of the film therefore reduces to:

$$\pm\frac{2{\cdot}02}{\sqrt{2}} = \pm 1{\cdot}43\ \mu$$
$$= \pm 0''{\cdot}068 \text{ on an astrographic plate.}$$

The images of stars on the plates appeared to be rather more irregular than is usually the case with astrographic plates. The errors of bisection were, in consequence, larger than when well-defined points are observed. It did not seem worth while to carry the measurements further, since more reliable results could, with fewer measures, be derived from the comparison of negatives on which well-defined lines have been impressed from the same

réseau. If the comparison be made by measuring the intervals, these may also be compared on the same plate and a test of the divisions of the réseau afforded. But in this case a source of error is introduced which does not affect measurements of the co-ordinates of a point by reference to the réseau scale (since in the one case the réseau interval is the quantity measured, and in the other it is the unit of measure).

If the horizontal lines on the plate make a small angle θ_1 with the plane of motion of the slide, the error in any x resulting from the measured réseau intervals will be

$$-\frac{\theta_1 x^2}{f}.$$

There will also be a similar error due to the small angle θ_2 between the horizon line on the réseau plate and its projected image on the photographic plate. If θ be the sum of these angles, the correction to a réseau interval lp on the plate will be

$$\frac{\theta x^2_p}{f}-\frac{\theta x^2_{p-1}}{f}=\frac{l(x_p+x_{p-1})\theta}{f}.$$

The observation equations are then of the form

$$L_p-\frac{l(x_p+x_{p-1})}{f}\theta-l_p=v_1.$$

If, for the purpose of determining θ, we treat the réseau errors as accidental, and from each equation with a positive value of x subtract the corresponding equation with a negative value, we get

$$-2a_1\theta-l_1+l_n=v'_1,$$
$$-2a_2\theta-l_2+l_{n-1}=v'_2,$$
$$\cdot\quad\cdot\quad\cdot\quad\cdot\quad\cdot\quad\cdot\quad\cdot\quad\cdot\quad\cdot$$

from which the most probable value of θ is

$$\theta=\frac{a_1(l_n-l_1)+a_2(l_{n-1}-l_2)+\ \dots\ .}{2[a^2]}.$$

Substituting this value of θ in the original observation equations, the corrections to the réseau intervals follow at once.

Another small correction might be applied on account of the aberration caused by the thickness of the glass plate through which the réseau is projected upon the film, but its computed value being only 0·06 μ, for a maximum at outer réseau intervals, it was disregarded.

The réseau intervals along the horizon line of two plates were measured twice with the micrometers. Each end-reading was the mean of bisections with the screw moving to the right and to the left. The measures, corrected for inclination θ of the plates on the slides (which was $-0' \, 12''$ for plate 10

and $-2' 33''$ for plate 9), gave results as under, the two outer intervals which might be affected by frilling of the film at its edges being omitted :

Réseau interval.	Plate 10, I–II.	Plate 9, I–II.	Difference, 10–9.	Mean of 10 and 9, 5000 μ.
	μ	μ	μ	μ
45–50	+1·16	+1·63	−2·77	−1·55
50–55	+0·66	+1·86	−2·02	−2·23
55–60	−0·69	+0·94	−1·91	−2·07
60–65	−2·16	−0·89	−2·91	−0·23
65–70	+0·06	+0·56	−4·00	+1·59
70–75	+0·58	−0·03	+0·45	−1·55
75–80	+0·26	−2·44	+4·61	+0·38
80–85	+0·84	−0·84	+0·47	+1·54
85–90	+0·07	−0·09	+0·14	+2·22
90–95	−1·01	−0·01	+1·53	+1·46
95–100	+1·25	−0·48	+2·56	+0·68
100–105	−0·56	−0·31	+0·80	+1·52
105–110	−2·93	−1·11	+5·15	+1·03
110–115	−2·09	+1·72	+2·03	+2·62
115–120	−1·34	−2·63	+3·95	+0·62
120–125	+1·67	+0·41	+1·98	+0·26
125–130	+1·14	+0·59	+2·09	−1·49
130–135	−0·47	+0·66	+4·18	−0·19
135–140	−0·66	−0·09	−4·76	+0·31
140–145	+1·19	+1·52	−4·68	−1·22
145–150	+1·59	+0·52	−1·83	−1·38
150–155	+1·59	−1·37	−5·00	−2·32
Sums of squares	36·93	31·60	216·00	48·52

The measures of plate 10 gave clear indication of systematic error, due to a residual influence on the runs of the curvature of the plate. The runs remain constant for elements of the plate at different distances from the réseau plane, but will vary slightly with the inclination of these elements and their distance from the centre of the plate. This effect may be eliminated whenever great precision is desired by reading both réseau lines and correcting for runs in the usual way. But as a rule, and for present purposes, it will be sufficient to include this in the accidental errors. Let

r_1 = p.e. of a complete measurement (mean of I and II) of a réseau interval on a plate.

r_2 = p.e. from distortion of the film (including error inherent to the photographic image).

r_3 = p.e. of division of a réseau interval.

The first two columns give differences between the two measures, I and II, of the same réseau interval on the same plate. From plate 10,

$$r_1 = \pm 0{\cdot}6745\sqrt{\frac{36{\cdot}93}{4\times 21}} = \pm 0{\cdot}45\ \mu;$$

and from plate 9,

$$r_1 = \pm 0{\cdot}6745\sqrt{\frac{31{\cdot}60}{4\times 21}} = \pm 0{\cdot}41\ \mu.$$

Mean $\pm 0{\cdot}43\ \mu$.

From the third column, giving the differences between complete measures of corresponding réseau intervals on different plates,

$$\sqrt{r_1^2 + r_2^2} = \pm 0{\cdot}6745\sqrt{\frac{216}{2\times 21}} = \pm 1{\cdot}53\ \mu,$$

whence

$$r_2 = \sqrt{(1{\cdot}53)^2 - r_1^2} = \pm 1{\cdot}47\ \mu.$$

This value agrees well with the value $\pm 1{\cdot}43\ \mu$ which was derived from the comparison of star plates.

From the last column, giving the means of the complete measures,

$$\sqrt{\frac{r_1^2 + r_2^2 + r_2^2}{2}} = \pm 0{\cdot}6745\sqrt{\frac{48{\cdot}52}{21}} = \pm 1{\cdot}03\ \mu.$$

But

$$\sqrt{\frac{r_1^2 + r_2^2}{2}} = \pm\frac{1{\cdot}53}{\sqrt{2}} = \pm 1{\cdot}08\ \mu.$$

The measures, therefore, give no indication of sensible accidental error of graduation of the réseau. Any systematic error remaining is eliminated in the correction for distortion of the lens, the distortion having been determined with reference to the réseau scale.

The effect of distortion of the film on the measures will be :

In a plate co-ordinates (scale read on both R-lines),

$$\pm\frac{1{\cdot}03}{\sqrt{2}} \pm 1{\cdot}03 = \pm 1{\cdot}26\ \mu.$$

In a stereoscopic difference, $\pm 1{\cdot}26\sqrt{2} = \pm 1{\cdot}78\ \mu$.

In order to form an estimate of the advantage of using a réseau, the distances of the vertical réseau lines from the centre of one plate were compared, using the measuring-machine simply as a comparator, with the corresponding distances on five other plates taken at random. The differences found were :

Réseau line.	Plate 10–9.	Plate 10–20.	Plate 10–18.	Plate 10–19.	Plate 10–7.
	μ	μ	μ	μ	μ
45	+ 3·4	−31·8	+43·5	+22·0	+55·3
50	− 7·5	−41·0	+34·5	+18·2	+48·0
55	−15·5	−44·0	+35·8	+11·2	+34·3
60	−24·0	−50·8	+26·2	+ 8·5	+13·5
65	−20·8	−47·9	+25·2	+ 7·5	+12·6
70	−23·7	−46·0	+15·5	+ 4·5	− 3·5
75	−18·7	−36·4	+19·3	+ 0·5	+ 4·5
80	−17·6	−28·7	+13·0	+ 6·5	+ 0·2
85	−11·0	−25·3	+ 7·0	+ 5·5	+ 7·5
90	−15·4	−17·0	+ 4·5	+ 6·0	+ 4·5
95	− 2·0	− 6·0	0·0	+ 6·5	+ 2·0
100	− 0·8	0·0	0·0	+ 0·7	0·0
105	+ 8·4	+ 5·2	0·0	+ 0·5	+ 8·0
110	+18·2	+12·1	+ 2·0	− 0·3	+ 8·1
115	+25·0	+18·3	+ 4·0	+ 6·5	+ 6·9
120	+21·2	+26·2	+ 1·5	+ 9·3	+10·7
125	+19·5	+26·0	+ 7·2	− 3·4	+13·1
130	+25·5	+26·0	+11·5	+ 2·0	+23·1
135	+29·2	+26·9	+27·0	+ 1·0	+18·6
140	+28·0	+21·6	+34·5	+ 2·0	+19·7
145	+28·0	+22·3	+37·0	− 2·9	+25·3
150	+26·2	+13·7	+51·2	+ 3·5	+28·2
155	+20·0	+ 6·0	+66·0	− 2·7	+30·6

It will be seen that with plates of contrary curvature, such as 20 and 7, the error in a stereoscopic difference derived from orthogonal measures of the plates with reference to a réseau may amount to 100 μ, so that in this case the use of a réseau decreases the maximum error fifty-fold. The use of a réseau is therefore imperative for any precision if commercial plates are to be used and linear methods of measurement adhered to.

More simply, examining a number of plates against a straight edge, some were found to have a departure from straightness of fully 0·2 mm., which corresponds to a possible error of 78 μ on the margins of a single plate.

Distortion of the Lens.—The best method of determining the optical distortion of a lens would perhaps be to place it on a turntable with a plane scale at its principal focus, and measure the rotations of the assemblage for successive bisections of the division lines with a fixed collimating telescope placed in front of the lens. By arranging the measures suitably, and converting the observed angles into their tangents, the reduction would take much the same form as in the investigation of the errors of division of a line measure or in the calibration of thermometers.

It was, however, not convenient to use this method, and another was devised in which the camera is rotated through a definite angle and plates exposed in each position. Knowing the angle of rotation, the position of any point on the second plate may be computed from measurements on the first, and any discrepancy found will be due to :

(1) Differences in the angular distortion of the lens.
(2) Error in the focal length assumed.
(3) Error in the zero of the plate co-ordinates.
(4) Distortion of the film and error inherent in the photographic image.
(5) Errors of division of the réseau.
(6) Curvature of the réseau.
(7) Errors of measurement.

The method of measurement eliminates error due to curvature or tilt of the plate. Error (2) in the focal length may be eliminated by expressing the distortion in terms of the focal length. Errors (4) and (5) already investigated may be treated as accidental and included with error (7). (3) is the same in both plates, and will form the first term of the correction for distortion. Error (5) was previously found to be insensible, and error (6) is avoided by dividing the réseau on an optically worked plane surface.

An accurate knowledge of the optical distortion is chiefly needed in respect of the images of distant points, since the effect on computed positions of errors in the measures is then greater than with nearer points. On the photographs such distant points tend to approximate with the horizon line. It is therefore of special importance to determine the distortion in a horizontal diameter. For other diameters it will be sufficient to consider it a function of r.

If the distortion be of the form

$$dr^2+er^3+gr^4,$$

the correction to x on account of distortion will be

$$x(dr+er^2+fr^3),$$

and the total correction may be written

$$f(x,\ z)=ax+bx^2+cxz+x(dr+er^2+gr^3).$$

The first term gives simply a change of scale, and may be eliminated by correcting the assumed value of the focal length. The third results from a tilt of the optical axis of the lens relatively to the horizon plane, and the second from a tilt relatively to the vertical plane, passing through the z axis of the plate. These deviations of the optical axis are due to slight errors in centering the lenses of the objective. When their centres

of curvature are not exactly in a straight line a pair of lenses will act as a combination of a lens and a prism.

No constant term for error in the co-ordinates of the centre of the plate is added because the centre was determined accurately by direct optical means already described, and any further correction from the observation equations would have had a very small weight in comparison.

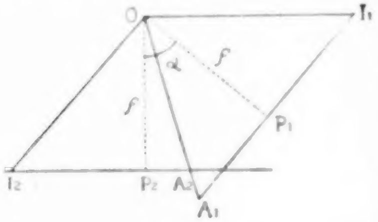

FIG. 10.

Let I_1A_1, I_2A_2 (fig. 10) be the relative position of the pair of plates, O the optical centre of the lens, a the angle of rotation of the camera, and A_1A_2 images of the same point on the two plates. Draw OI_1, OI_2, and OP_1, OP_2 parallel and perpendicular respectively to I_1A_1 and I_2A_2. From a simple proposition in projective geometry (since the triangles OI_1A_1 and A_2I_2O are similar)—

$$I_2A_2 = -\frac{k}{I_1A_1} \text{ where } k = OI_1 \,.\, OI_2 = \frac{f^2}{\sin^2 a}$$

$$x_2 - f\cot a = -\frac{k}{x_1 + f\cot a},$$

or

$$x_2 - A = -\frac{k}{x_1 + A}.$$

Differentiating,

$$dx_2 = \frac{k}{(x_1+A)^2}dx_1 = m dx_1.$$

Let l_1 be difference between the computed and observed values of x_2. We have then observation equations of the form

$$\triangle x_2 - m\triangle x_1 - l_1 = v_1 \quad (l_1 = C - O),$$

or

$$ax_2 + bx_2^2 + cx_2z_2 + x_2(dr_2 + er_2^2 + gr_2^3)$$
$$- m[ax_1 + bx_1^2 + cx_1z_1 + x_1(dr_1 + er_1^2 + gr_1^3)] - l_1 = v_1,$$

reducing to

$$(x_2 - mx_1)a + (x_2^2 - mx_1^2)b + (x_2z_2 - mx_1z_1)c$$
$$+ (x_2r_2 - mx_1r_1)d + (x_2r_2^2 - mx_1r_1^2)e$$
$$+ (x_2r_2^3 - mx_1r_1^3)g - l_1 = v_1,$$

from a sufficient number of which we may determine the values of the coefficients, subject to the condition that the sum of the squares of the residuals v is a minimum.

Two plates were exposed before and after rotation of the camera through a definite angle by pointing its telescope successively at two marks of approximately equal altitudes. The angle between these, measured with a micrometer theodolite, was found to be 18° 27′ 29″·40. The view was chosen to include sharply defined buildings along the horizon line. From this choice of comparatively near objects, a small correction $\Delta x = -0{\cdot}0669e$ (Δx in microns, e in mm.) to the x's of the first plate, owing to the displacement of the camera lens in the second position, was introduced. The value assumed for the focal length was 139·600 mm., whence the values of the constants k and A were

$$k = 194408{\cdot}66, \quad \log 5{\cdot}2887156{,}0,$$
$$A = 418{\cdot}2350, \quad ,, \ 2{\cdot}6214203{,}3.$$

Eighty-two objects were measured near the horizon line and 16 more near the corners of the plate to provide for the coefficients in xz. To reduce the labour of the formation of the observation and normal equations the points were chosen in groups within an x-distance of generally 2 mm.

Group.	No. of points.	z_1.	x_1.	z_2.	x_2. Observed.	x_2. Computed.	C–O. μ.
I	5	+ 3·21	57·1788	+ 2·94	9·1431	9·3095	+166·36
II	5	+ 2·24	53·2572	+ 2·09	5·7602	5·9085	+148·34
III	3	− 0·36	48·8990	− 0·37	1·9404	2·0615	+121·13
IV	5	+ 1·71	46·3377	+ 1·56	− 0·3466	− 0·2339	+112·74
V	4	− 0·49	42·9933	− 0·38	− 3·3603	− 3·2683	+ 92·02
VI	4	+ 0·30	39·0014	+ 0·29	− 7·0212	− 6·9473	+ 73·87
VII	9	+ 3·28	34·4793	+ 3·16	−11·2519	−11·1946	+ 57·25
VIII	4	+ 1·05	30·9181	+ 1·96	−14·6779	−14·6290	+ 48·90
IX	3	+ 3·01	28·4265	+ 2·94	−17·0616	−17·0137	+ 47·87
X	5	+ 3·01	29·9600	+ 2·96	−20·4581	−20·4204	+ 37·72
XI	5	+ 0·42	20·8789	+ 0·36	−24·5352	−24·4964	+ 38·76
XII	5	+ 0·03	15·4063	+ 0·02	−30·1250	−30·0843	+ 40·72
XIII	3	− 2·00	11·2599	− 2·10	−34·4609	−34·4104	+ 50·53
XIV	6	− 0·26	6·3965	− 0·29	−39·6546	−39·5991	+ 55·48
XV	5	+ 2·99	1·0390	+ 3·10	−45·5137	−45·4455	+ 68·22
XVI	3	+ 2·91	− 0·8877	+ 2·98	−47·6700	−47·5859	+ 84·10
XVII	3	+ 3·31	− 4·0196	+ 3·35	−51·2066	−51·1076	+ 99·00
XVIII	5	+ 3·00	− 7·9413	+ 3·19	−55·7148	−55·5945	+120·28
XIX	4	+35·23	+44·9519	+33·45	− 1·6060	− 1·4862	+119·80
XX	4	+34·10	+50·7615	+31·97	+ 3·5651	+ 3·7141	+149·00
XXI	4	+32·64	− 1·0500	+34·54	−47·8702	−47·7674	+102·83
XXII	4	+30·37	− 4·8348	+32·43	−52·1528	−52·0331	+119·65

The co-ordinates of each point on the second plate were computed from the measurements on the first, but the observation equations were formed for only each of 22 groups arranged, the weight of each equation being taken as proportional to the number of points from the measurements of which it was formed. This simplification causes no sensible loss of accuracy, the assumption being not that the changes in the function giving the computed values are linear for the interval, but only that the changes in the *correction* are such, and this is sufficiently true within the errors of measurement.

The measures were (means of groups and x_1 being corrected for displacement of the lens) in millimetres, except C—O in microns (see table, p. 35).

The observation equations for the groups become :

Observation Equations $x\sqrt{p}$.

Equation.	*a.*	*b.*	*c.*	*d.*	10*e.*	100*g.*	*l.*	
1	+4·005	+27·290	+ 1·310	+27·293	+16·040	+ 9·232	+166·360	$=v_1\sqrt{p_1}$
2	+4·082	+24·475	+ 0·923	+24·479	+13·214	+ 7·056	+148·340	$=v_2\sqrt{p_2}$
3	+3·226	+16·482	− 0·116	+16·483	+ 8·074	+ 3·948	+ 93·880	$=v_3\sqrt{p_3}$
4	+4·210	+19·345	+ 0·719	+19·365	+ 8·978	+ 4·162	+112·740	etc.
5	+3·813	+15·000	− 0·184	+15·208	+ 6·497	+ 2·793	+ 82·270	
6	+3·869	+12·202	+ 0·028	+13·084	+ 4·962	+ 1·925	+ 66·040	
7	+5·891	+13·416	+ 1·915	+16·946	+ 5·464	+ 1·846	+ 76·720	
8	+3·974	+ 6·319	+ 0·536	+10·178	+ 2·836	+ 0·831	+ 43·720	
9	+3·469	+ 3 847	+ 1·035	+ 8·426	+ 2·151	+ 0·570	+ 37·100	
10	+4·517	+ 1·982	+ 1·350	+10·441	+ 2·436	+ 0·573	+ 37·720	
11	+4·559	− 1·627	+ 0·176	+10·437	+ 2·404	+ 0·557	+ 38·760	
12	+4·605	− 6·621	+ 0·001	+11·533	+ 3·113	+ 0·882	+ 40·720	
13	+3·590	− 8·169	− 0·745	+10·271	+ 3·303	+ 1·112	+ 39·160	
14	+5·097	−16·731	− 0·775	+17·759	+ 6·885	+ 2·724	+ 60·750	
15	+4·666	−20·700	+ 1·445	+20·795	+ 9·472	+ 4·318	+ 68·220	
16	+3·618	−17·604	+ 1·079	+17·621	+ 8·428	+ 4·025	+ 65·180	
17	+3·616	−20·183	+ 1·212	+20·183	+10·442	+ 5·363	+ 76·720	
18	+4·654	−30·308	+ 1·502	+30·310	+17·282	+ 9·674	+120·280	
19	+3·785	+16·344	+13·308	+21·276	+12·038	+ 6·836	+107·100	
20	+3·691	+20·244	+12·656	+23·499	+14·667	+ 9·064	+133·210	
21	+4·175	−20·475	+14·440	+24·921	+14·801	+ 8·766	+ 91·930	
22	+4·171	−20·075	+13·627	+27·120	+17·119	+10·655	+106·970	

The resulting normal equations are :

a.	*b.*	*c.*	*d.*	10*e.*	100*g.*	*l.*	
+ 386·51	− 1·48	+ 264·58	+1656·55	+ 785·94	+ 396·85	+ 7476·09	=0
− 1·48	+6735·43	− 146·49	− 157·96	− 136·96	− 94·92	+ 6028·90	=0
+ 264·58	− 146·49	+ 749·63	+1538·10	+ 902·03	+ 532·26	+ 6940·91	=0
+1656·55	− 157·96	+1538·10	+8057·29	+4128·07	+2192·37	+37186·57	=0
+ 785·94	− 136·96	+ 902·03	+4128·07	+2207·38	+1205·23	+19253·61	=0
+ 396·85	− 94·92	+ 532·26	+2192·37	+1205·23	+ 670·38	+10283·68	=0

Their solution gives : $a = +0{\cdot}15495$, $d = -3{\cdot}6902$,
$b = -1{\cdot}01935$, $10e = +0{\cdot}488$,
$c = +1{\cdot}34102$, $100g = -5{\cdot}450$.

Substituting these values in the observation equations, the residuals $v\sqrt{p}$ and their squares pvv are :

	$v\sqrt{p}$.	pvv.		$v\sqrt{p}$.	pvv.		$v\sqrt{p}$.	pvv.
1	−2·283	5·21	9	+1·955	3·82	17	+0·868	0·75
2	+2·923	8·54	10	−2·253	5·08	18	−2·230	4·97
3	−0·980	0·96	11	+0·982	0·97	19	−1·022	1·04
4	+4·874	23·76	12	+2·337	5·46	20	+1·160	1·35
5	−0·848	0·72	13	+4·694	22·03	21	+0·297	0·44
6	−2·113	4·46	14	+0·536	0·29	22	+0·637	0·09
7	−3·404	11·59	15	−3·667	13·45			
8	−2·090	4·37	16	+2·285	5·22		$[pvv] = 124{\cdot}55$	

From the investigation of the errors of the réseau and of the distortion of the film we had :

r_1 = p.e. of the complete measurement of a length on a plate $= \pm 0{\cdot}43\ \mu$.

r_2 = p.e. of the distance, resulting from distortion of the film (including error inherent in the photographic image) $= \pm 1{\cdot}47\ \mu$.

For a group of 5 points the probable error of the function of the measure (nearly the mean for the group) which enters the equations will be :

$$\frac{0{\cdot}43}{\sqrt{5}} \pm \frac{1{\cdot}47}{\sqrt{2}} \pm \frac{1{\cdot}47}{\sqrt{2\times 5}} = \pm 1{\cdot}15\ \mu,$$

and the resulting p.e. for the difference C − O on the second plate :

$$\pm 1{\cdot}15\sqrt{2} = \pm 1{\cdot}62\ \mu.$$

From the residuals of the group equations the p.e. due to uncorrected distortion of the lens and errors of measurement is for a group of 5 points of weight unity :

$$r = \pm 0{\cdot}6745\sqrt{\frac{[pvv]}{n-6}} = \pm 0{\cdot}6745\sqrt{\frac{124{\cdot}55}{22-6}} = \pm 1{\cdot}77\ \mu.$$

The p.e., which may be attributed to uncorrected distortion of the lens alone, is therefore :

$$\pm\sqrt{(1{\cdot}77)^2-(1{\cdot}62)^2} = \pm 0{\cdot}71\ \mu,$$

or, for either plate,

$$\pm\frac{0{\cdot}71}{\sqrt{2}} = \pm 0{\cdot}5\ \mu.$$

The groups were not all of 5 points, but a more rigorous computation would scarcely affect this value.

The corrections for distortion are finally (Δx, Δz in microns; x, z in cm.):

$$\begin{aligned}\Delta x &= +0{\cdot}1549x - 1{\cdot}0193x^2 + 1{\cdot}3410xz \\ &\quad -3{\cdot}6902xr + {\cdot}04880xr^2 - {\cdot}05450xr^3. \\ \Delta z &= +0{\cdot}1549z + 1{\cdot}3410z^2 - 1{\cdot}0193xz \\ &\quad -3{\cdot}6902zr + {\cdot}04880zr^2 - {\cdot}05450zr^3.\end{aligned}$$

The first term is eliminated by correcting the assumed focal length of 139·600 mm. by $-0{\cdot}00001459f = -0{\cdot}00216$ mm. The "standard" focal length then becomes 139·5978 mm. at 15° C. This is the distance, on the réseau scale, of the plane of the réseau from the back nodal point of the lens, for rays making a small angle with the optical axis. At temperatures other than 15° C. there is a change in this focal length of $0{\cdot}000014f = 0{\cdot}00195$ mm. for each 1° C., the increment resulting from the difference in the coefficients of expansion of aluminium and glass.

The corrections to x and z for distortion were computed for every 5 mm. in x and 10 mm. in z. A table of these values may be used for the application of the corrections, but on account of the double interpolation needed for intermediate values of x and z, it was found more convenient to use a diagram of curves of equal distortion for every 10 microns. The curves of the corrections to the x's being nearly orthogonal to those for the z's, both sets are conveniently represented on a single diagram. The corrections may then be estimated at sight to the nearest micron, with sufficient accuracy for practical applications.

The unsymmetrical terms of the distortion function being

$$\text{for } x, \quad bx^2 + cxz,$$
$$\text{for } z, \quad cz^2 + bxz,$$

could also be eliminated by applying rotations α and β, making

$$bx^2 = -\frac{\alpha x^2}{f} \text{ and } cz^2 = -\frac{\beta z^2}{f}$$

and

$$b = -\frac{\alpha}{f},\ c = -\frac{\beta}{f} \text{ and } \alpha = -bf,\ \beta = -cf.$$

But these rotations also add increments to the co-ordinates of $-f\alpha$, $-f\beta$, so that corrections of $+f\alpha$, $+f\beta$ to the co-ordinates are still needed. We have then

$$\Delta x = -f\alpha\left(1 + \frac{x^2}{f^2}\right) - \frac{\beta xz}{f},$$

$$\Delta z = -f\beta\left(1 + \frac{z^2}{f^2}\right) - \frac{\alpha zx}{f}.$$

reducing to

$$\triangle x = +bx^2 + cxz - fa,$$
$$\triangle z = +cz^2 + bxz - f\beta.$$

In the particular case considered,

$$a = -bf = +4'\ 53''{\cdot}5,$$
$$\beta = -cf = -6'\ 26''{\cdot}1.$$

This is the measure of the lateral and vertical deviations of an axial ray passing through the lens. If the rotations a and β are applied by adjusting by these amounts the telescope collimation and the level, the plate co-ordinates will still require corrections of

$$\triangle x = +0{\cdot}1991 \text{ mm.},$$
$$\triangle z = -0{\cdot}2613 \quad ,,$$

which may again be eliminated by displacing the camera lens these distances in its horizontal and vertical slides.

The curves of distortion along a horizontal diameter are shown in fig. 11. As might be expected from the circumstance that the back lens of the combination is of greater focal length than the front one, the distortion is of the "pin-cushion" type, the sag of a straight line 5 cm. above the x-axis being 0·1077 mm. in 12 cm.

The investigation of the distortion which is outlined above proved somewhat laborious, but it was gratifying to find that the distortion of a good lens may be satisfactorily represented by a function of the radius from the centre of the plate plus the effect of a tilt of the plate. Accidental errors in the optical distortion are then almost negligible in comparison with those due to the distortion of the film and the impression of the image. The result is of importance, for were it otherwise no accurate measurement of a plate, independently of the lens it was taken with, would be possible.

The lens selected was of a type recommended for survey work, but it seems very probable that a symmetrical lens of equally good workmanship would have given better results. It may even be that the distortion of a symmetrical lens would be reduced to a negligible quantity by fitting an adjustable diaphragm, of which the relative distance from the front and the back lenses could be varied within small limits. The distortions of the front and back halves of a symmetrical doublet are of the opposite "pin-cushion" and "barrel" types, but they do not compensate strictly except for magnification 1. With a small stop, however, the distortions will vary with the position of the stop, so that if the residual effect for distant objects is small, it should be possible to very nearly balance the two distortions by adjusting the diaphragm to some position not exactly midway between

the lenses. Any remaining error could then be still further reduced by choosing a value for the focal length which makes the distortion zero at three points of a diameter, as shown by the lower curve in fig. 11.

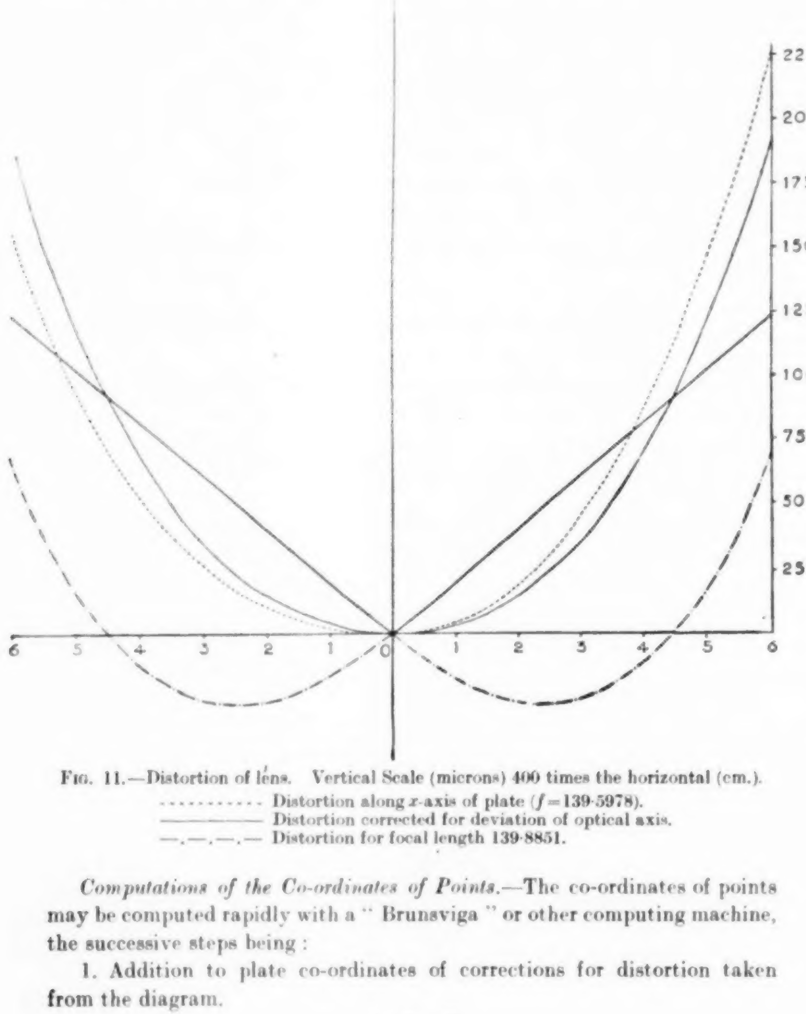

Fig. 11.—Distortion of lens. Vertical Scale (microns) 400 times the horizontal (cm.).

.... Distortion along x-axis of plate ($f = 139 \cdot 5978$).

———— Distortion corrected for deviation of optical axis.

—.—.—.— Distortion for focal length 139·8851.

Computations of the Co-ordinates of Points.—The co-ordinates of points may be computed rapidly with a "Brunsviga" or other computing machine, the successive steps being :

1. Addition to plate co-ordinates of corrections for distortion taken from the diagram.

2. $$e = x_a - x_b.$$

3. $$m = \frac{b}{e}.$$

4. $Y = mf$.
5. $X = mx$.
6. $Z = mz$.

Thus there are only two settings of numbers on the machine, first b, then m. b being a constant for the pair of plates, the values of m for a number of points may be computed before the setting of the machine is changed.

7. Addition of correction to z for curvature and refraction, taken from a small table inserted here for reference. The correction is

$$\frac{s^2}{r}\left(\frac{1-2k}{2}\right).$$

For a mean value of the coefficient of refraction, $k = 0{\cdot}07$ and X and Y in kilometres, this reduces to

$$0{\cdot}067416(X^2+Y^2).$$

If the probable error of the coefficient of refraction is taken to be $\pm 0{\cdot}005$, the p.e. of the correction from the table becomes about 1 per cent. of its amount.

Table of Corrections for Curvature and Refraction ($k = 0{\cdot}07$)

Y.	X in kilometres.			Y.	X in kilometres.				Y.	X in kilometres.					
	0.	1.	2.		0.	2.	3.	4.		0.	2.	3.	4.	5.	6.
0·2	0·00			5·2	1·8	2·1	..	..	10·2	7·0	7·3	7·6	8·1	8·7	
0·4	0·01			5·4	2·0	2·2	..	..	10·4	7·3	7·6	7·9	8·4	9·0	
0·6	0·02			5·6	2·1	2·4	..	..	10·6	7·6	7·8	8·2	8·7	9·3	
0·8	0·04			5·8	2·3	2·5	..	..	10·8	7·9	8·1	8·5	8·9	9·5	
1	0·08			6	2·4	2·7	3·0	..	11	8·2	8·4	8·8	9·2	9·8	
1·2	0·10			6·2	2 6	2·9	3·2	..	11·2	8·5	8·7	9·1	9·5	10·1	
1·4	0·13			6·4	2·8	3·0	3·4	..	11·4	8·8	9·0	9·4	9·8	10·4	
1·6	0·17			6·6	2·9	3·2	3·5	..	11·6	9·1	9·3	9·7	10·2	10·8	
1·8	0·22			6·8	3·1	3·4	3·7	..	11·8	9·4	9·7	10·0	10·5	11·1	
2	0·27	0·34		7	3·3	3·6	3·9	4·4	12	9·7	10·0	10·3	10·8	11·4	12·1
2·2	0·33	0·39		7·2	3·5	3·8	4·1	4·6	12·2	10·0	10·3	10·6	11·1	11·7	12·5
2·4	0·39	0·46		7·4	3·7	4·0	4·3	4·8	12·4	10·4	10·6	11·0	11·4	12·0	12·8
2·6	0·46	0·52		7·6	3·9	4·2	4·6	5·0	12·6	10·7	11·0	11·3	11·8	12·4	13·1
2·8	0·53	0·60		7·8	4·1	4·4	4·7	5·2	12·8	11·0	11·3	11·7	12·1	12·7	13·5
3	0·61	0·67	0·88	8	4·3	4·6	4·9	5·4	13	11·4	11·7	12·0	12·5	13·1	13·8
3·2	0·69	0·76	0·96	8·2	4·5	4·8	5·1	5·6	13·2	11·7	12·0	12·4	12·8	13·4	14·2
3·4	0·78	0·85	1·05	8·4	4·8	5·0	5·4	5·8	13·4	12·1	12·4	12·7	13·2	13·8	14·5
3·6	0·87	0·94	1·14	8·6	5·0	5·3	5·6	6·1	13·6	12·5	12·7	13·1	13·5	14·2	14·9
3·8	0·97	1·04	1·24	8·8	5·2	5·5	5·8	6·3	13·8	12·8	13·1	13·4	13·9	14·5	15·3
4	1·08	1·15	1·35	9	5·5	5·7	6·1	6·5	14	13·2	13·5	13·8	14·3	14·9	15·6
4·2	1·19	1·26	1·46	9·2	5·7	6·0	6·3	6 8	14·2	13·6	13·9	14·2	14·7	15·2	16·0
4·4	1·31	1·37	1·57	9·4	6·0	6·2	6·6	7·0	14·4	14·0	14·2	14·6	15·1	15·7	16·4
4·6	1·43	1·49	1·70	9·6	6·3	6·5	6·8	7·3	14·6	14·4	14·6	15·0	15·4	16·1	16·8
4·8	1·55	1·62	1·82	9·8	6·5	6·7	7·1	7·6	14·8	14·8	15·0	15·4	15·8	16·5	17·2
5	1·70	1·75	1·96	10	6·7	7·0	7·3	7·8	15	15·2	15·4	15·8	16·2	16·9	17·6

The use of computation forms, on which the plate measures can be entered directly as they are made, saves time and reduces the chances of error. An example of the computation for a point follows :—

Point No. 262.		Plates 13 and 15.		b=340·110 metres.	
143·304	+43·304	− 74=	+43·230	b/e 29·808	Y+4161·3
154·776	+54·776	−136=	+54·640	Z′ 833·7	X+1288·6
11·472		− 62	11·410	+ 1·2	Z+ 834·9
128·04	+28·04	− 7=	27·97		h_0 120·8
					h = 955·7

143·304 and 154·776 are the measured plate x's, and 128·04 the plate z. −74, −136, and −7 are the corrections in microns to x_a, x_b, and z for distortion taken from the diagram. +1·2 is the correction for curvature and refraction, and 120·8 is the height of the origin of Z.

With a "Brunsviga" machine the speed of the computation, after corrections for distortion have been applied, is at the rate of about 20 points per hour, using computation forms as above.

The time required for the complete operation is as follows :—

	Points per hour.
Measurement of plate co-ordinates	25
Application of corrections	120
Computing	20
Plotting	200
Or for 100 points :	
Measuring	4 hours.
Corrections	0·83
Computing	5
Plotting	0·50
	Say 10 hours.

Errors of the Method.—Differentiating the expressions for X, Y, Z, we have

$$dY=-\frac{bf}{e^2}de,$$

$$dX=\frac{b}{e}dx-\frac{bx}{e^2}de,$$

$$dZ=\frac{b}{e}dz-\frac{bz}{e^2}de,$$

which may be written

$$dY = -\frac{Y}{e}de,$$

$$dX = \frac{b}{e}dx - \frac{X}{e}de,$$

$$dZ = \frac{b}{e}dz - \frac{Z}{e}de.$$

We have already seen that the p.e. of a bisection with either micrometer of the machine varies from $\pm 0{\cdot}27\,\mu$ for a mark of best definition to $\pm 0{\cdot}43\,\mu$ for a réseau line. Ordinary topographical objects, being usually ill-defined and irregular, can seldom be bisected accurately with each eye singly, but, stereoscopically, the adjustment of their apparent distance with that of the index can be effected with great comparative delicacy. As with single marks, the p.e. of stereoscopic bisection also varies with the class of object, as shown in the table below:

		No. of observations.
Marks on buildings	$\pm 1{\cdot}19$	20
Trees and other definite marks	$\pm 1{\cdot}76$	40
Rocks, tops of hills, and other less definite marks	$\pm 2{\cdot}65$	40

The p.e. of the stereoscopic bisection of an ordinary topographical point, without regard to the character of the object, may therefore be taken as $\pm 2{\cdot}0\,\mu$.

There are other sources of error, some of which, such as the orientation of the base, are indirect, but it will be convenient to include all in the errors of the plate measures. Collecting the results so far arrived at, we get the following analysis :—

Errors in Measurement of e.

	μ
p.e. of stereoscopic bisection	$\pm$ 2·0
Bisection of réseau lines $\pm 0{\cdot}43\sqrt{2} =$	$\pm$ 0·6
Distortion of the film and error inherent in the photographic image $1{\cdot}47\sqrt{2} =$	$\pm$ 2·1
Errors of scales and screws treated as accidental $\pm 0{\cdot}28\sqrt{2} =$	$\pm$ 0·4
Uncorrected distortion of lens and error in taking out correction from diagram $1{\cdot}1\sqrt{2} =$	$\pm$ 1·5
Error in length of the base line and in relative orientation of the pair of plates	$\pm$ 1·5
Errors due to insufficient adjustment for runs and difference in temperatures of exposure of the pair of plates, and residual errors estimated	$\pm$ 1·5
Combined probable error	$\pm$ 4·0

Errors in Measurement of x.

Error in actual measurement and in absolute orientation of the pair of plates and in that of the base line . .	$\pm 10\mu$

Errors in Measurement of z.

	μ
Error in estimation of tenths (from trials)	$\pm$ 3·0
Error in levelling and from unequal heating (1 division of the level $= 35\ \mu$)	$\pm$ 4·0
Uncorrected distortion of lens and error in taking out correction	$\pm$ 1·1
Distortion of film and photographic error	$\pm$ 1·5
Adjustment of level and of zero of the front scale, estimated	$\pm$ 4·0
Combined probable error	$\pm$ 6·7

The combined effect of all the errors on the measures is then, for an ordinary topographical object, p.e., $e = \pm 4\ \mu$; p.e., $x = \pm 10\ \mu$; p.e., $z = 7\ \mu$.

The probable error of the co-ordinates resulting from these values is for a mean x of 30 mm. and a mean z of 20 mm.

Y.	P.e. Y.	P.e. X.	P.e. Z.
Base 300 m.			
1,000 m.	0·1	0·1	0·1
2,000 ,,	0·4	0·2	0·1
3,000 ,,	0·9	0·3	0·2
4,000 ,,	1·5	0·4	0·3
5,000 ,,	2·4	0·6	0·4
6,000 ,,	3·4	0·8	0·6
7,000 ,,	4·7	1·1	0·8
8,000 ,,	6·1	1·4	1·0
9,000 ,,	7·7	1·8	1·2
10,000 ,,	9·5	2·2	1·4
11,000 ,,	11·5	2·6	1·7
12,000 ,,	13·7	3·1	2·0
Base 500 m.			
15,000 m.	12·9	3·0	2·0
Base 1000 m.			
20,000 m.	11·4	2·8	1·9

Range of the Method.—Let $\frac{1}{100}$th of an inch, or 0·25 mm., be the admissible error on the plan, and 12 km. the limiting value of Y. On the scale of the Canadian photographic surveys, $\frac{1}{40.000}$, the maximum error allowable will be 10 m. at 12 km. Then

$$\frac{\Delta Y}{Y}=\frac{1}{1200}=-\frac{\Delta e}{e}=\frac{0{\cdot}004}{e},$$

whence $e=4{\cdot}800$ mm. and $b=420$ m.

With this base, the area mapped with a plate of 120 mm. effective horizontal diameter and the lens of 139·6 focal length would be contained between the limiting circles at 12 km. and the front plane of the stereoscopic field at about 7 times the length of the base, and would amount to 51 sq. km. on either side of the base, or, more correctly, to the portion of that area not marked by interfering topographical features.

On the scale of $\frac{1}{40.000}$ the average p.e. of a contour line should then be only $\pm 0{\cdot}1$ mm. on slopes of more than 10°, but the actual error will be greater because the lines are drawn from a limited number of points. It will vary with the number of points of reference and the skill with which the contours are interpolated by sketching.

Test of the Method.—The first test was made on 26th August 1904, when plates were exposed at the ends of a base of 340·110 m. The view which is reproduced in fig. 1 (Plate IV) included a portion of Devil's Peak, near Cape Town, which had been surveyed independently and afforded a number

Distances.

No. of point.	No. of measures.	Plates 13 and 15.	Plates 14 and 16.	Diff. I–II.
236	1	4598·9	4600·0	−1·1
260	5	4269·9	4270·0	−0·1
262	5	4356·3	4358·3	−2·0
263	5	4423·8	4427·6	−3·8
264	3	2629·4	2630·4	−1·0
265	3	2630·1	2630·6	−0·3

Heights.

No. of point.	No. of measures.	Plates 13 and 15.	Plates 14 and 16.	Diff. I–II.
236	1	942·4	943·2	−0·8
260	1	830·4	831·0	−0·6
262	1	955·7	955·5	+0·2
263	1	1028·8	1028·9	−0·1
264	1	157·4	157·7	−0·3
265	1	157·4	157·8	−0·4

Differences of Direction.

	° ′ ″	Diff. from mean.
236	36.19.12	−43″
260	36.20.23	+28
262	36.20.1	+ 6
263	36.20.26	+31
264	36.19.38	−17
265	36.19.48	− 7

of checks. From the measurements of 266 points on the photographs, the map shown in fig. 2 (Plate IV) was drawn. Another pair of plates was exposed from the ends of a base of 409·120 m., one station being common to both bases, which differed in azimuth by 36° 19′ 55″. The comparison of the computed distances and heights of points common to both pairs of plates where they overlapped was (see table, p. 45).

The average probable errors derived from these differences are for an average distance of 3800 m.

	m.	P.e. from tables.
For single distances,	$\pm 0{\cdot}6$	$\pm$ 1·1
For single heights,	$\pm 0{\cdot}2$	$\pm$ 0·3
For single directions,	$\pm 13'' = 10\ \mu$	$\pm 10\ \mu$

The comparison of distances or heights of points of known position which could be identified on two pairs of plates comes out as follows :—

Point.	Plates 13 and 15.	By Survey.	Diff.
A distance)	5069·3	5070·6	−1·3 m.
B ,,	4053·2	4051·6	+1·6
Y (height)	998·7	991·1	−0·4
	Plates 7 and 8.		
A (distance)	5066·0	5070·6	−4·6
B ,,	4049·9	4051·6	−1·7

The heights of A and B were not obtainable from the survey, while the actual trig. station at Y (top of Devil's Peak) could not be identified on the plates, making, for Y, the height alone comparable.

Other checks are :

Five points, N O P Q R, on a road shown by the plan. The points are plotted from plate measurements, but the road from an entirely independent traverse which formed part of an earlier topographical survey.

Ten points, C D E F G H I K L M, on an upper path. In this case also the points are plotted from plate measurements and the path from an independent survey. It will be seen that in both cases all the points from the photographs are consistent with the independent survey within the limits of graphical accuracy.

Thus, in 38 cases in which comparisons could be made, the results show that the average errors are well within the limits indicated by the table of probable errors given previously, and therefore that no important source of error was overlooked in the discussion.

Stereocomparator.—Dr. Pulfrich, of Jena, devised at about the same time, and independently, a stereoscopic method of measurement, described in a paper in the Zeitschrift für Instrumentenkunde for March, May, and August 1902. To the instrument used for the measurement of plates he gives the name of "Stereocomparator." It differs somewhat in design from the measuring stereoscope of the author, and the measurements are referred not to a réseau but to independent metal scales recording the relative or absolute displacement of the plates on the machine. In consequence the plates cannot be measured directly when they are set at an inclination corresponding to that of the base line, which is the condition for combining correctly the pair of plates. An approximate combination is, however, obtained if one of the plates is moved vertically, whenever a measurement is made, until the point considered is at the same height on both plates.

According to Col. Laussedat (Bull. Soc. française de Photographie, t. xx, 1904), Baron von Hübl found it necessary when using the machine for topographical work to conduct the measurements at a constant temperature and to control the results by means of a large number of points determined by independent survey. Von Hübl concludes that the method is of limited usefulness in comparison with ordinary photogrammetry. He does not appear, however, to have taken into account the distortion of the lens, which may be considerable.

The accuracy of measurements made with a machine of the independent scale type is limited by :

(*a*) Errors in the relative setting of the plane of the plates in the camera and in the machine ; error in setting the corresponding reference lines on both plates truly parallel ; displacement of the horizontal zero setting, when measuring, if the auxiliary vertical slide moving one plate relatively to the other is not perfectly straight and accurately parallel with the reference marks on the supported plate.

(*b*) Errors in the straightness of the other slides introducing, from rotation, unequal displacement of the point observed and of the index of the recording scale placed some distance laterally.

(*c*) Differences between the temperatures at which the plates are exposed, at which they are set to zero in the machine, and at which each measurement is made. The effect of temperature changes is important, since small stereoscopic differences are determined from differences of large lengths, involving the coefficients of expansion of glass, steel, and brass.

(*d*) Curvature of the film. The picture is impressed as a projection from a point in the lens, but is measured orthogonally. The resulting error may be minimised by the use of plate glass to support the film, but it is not even then rendered negligible when the focal length is not large in comparison with the dimensions of the plate.

On the other hand, none of these sources of error affects measures made with the measuring stereoscope by reference to a réseau scale impressed in the camera. The results are then found to leave little to be desired in point of precision. Ordinary plates may be used and control surveys dispensed with. The speed of measurement is greater than with a scale machine, since all readings are made from the eye-piece, and one setting of the pair of plates, only necessarily approximate enough to produce stereoscopic combination, is sufficient for the whole of the measurements.

It is not expected that the method will displace any of those in present use. There is no universal method of surveying, and the skill of a surveyor is shown in nothing so much as in the correct choice of different methods under different conditions. But it is hoped, nevertheless, that the power and accuracy of the stereoscopic method will justify for it a place in the practice of topographical surveying.

Postscript.

Much confusion appears to be current regarding the origin of the method of Stereoscopic Surveying, as is evidenced by the following extracts :—

Encycl. Brit., 11th ed., art. "Stereoscope" (by C. Pulfrich), p. 899 : "A consequence of these instruments, which are chiefly important for military surveying, was the Pulfrich Stereocomparator, devised in 1901. The stereoscopic measuring-machine of H. G. Fourcade, of Cape Town (1902), is similar to this in many points."

The dates of first publication are Fourcade (1901) and Pulfrich (1902). It is, of course, most probable that the idea of the invention occurred to both some years earlier.

A. Laussedat, "Recherches sur les instrument, les méthodes et le dessin topographiques," vol. ii (Reprint from the Annales du Conservatoire des Arts et métiers, t. iv, 1903) :

Page 237 : "Tout ce qui se rapporte au Stéréocomparateur est extrait du Mémoire intitulé : Ueber neueren Anwendungen der Stereoskopie und über einen hiefur bestimmen Stereocomparator von Dr. Pulfrich in Iena, Sonderabdruck aus der Zeitschrift für Instrumentenkunde, 1901, H. 3, 5, 6, Julius Springer, Berlin, N."

Page 262: "L'appareil . . . sous tous les rapports rappelle le stéréocomparateur." *

There is here an unfortunate error in the date given, which should be 1902, not 1901. It is to be presumed that the error is simply due to a misprint, either in Laussedat, or in the title of the reprint from the Zeitschrift für Instrumentenkunde, H. 3, 5, 6, 1902. Given the correct date, the mention in the second extract of "a surely singular coincidence" becomes beside the mark.

A. R. Hinks, Geographical Journal, April 1922, p. 274: "*Brief history of the method.* . . . The difficulty was removed by the invention of the stereocomparator of Pulfrich about 1903. . . . The first application of the stereocomparator to topography seems to have been made at the Austrian Military-Geographical Institute by General von Hübl about 1904."

Here, more correctly, the dates are: the stereoscopic measuring-machine of H. G. Fourcade (1901), and the stereocomparator of Pulfrich (1902); and for the first stereoscopic survey, Fourcade (1904) and von Hübl (also 1904).

The following extracts may be read in this connection:—

H. G. Fourcade to Col. Laussedat, 5th June 1903: " . . . Je crois avoir trouvé une solution rigoureuse en théorie et suffisamment simple en pratique de la combinaison dans un métrostéréoscope de deux vues prises dans des plans différents. Cela permettrait l'emploi de clichés obtenus en ballon ou par cerf volant et rendrait la métrostéréoscopie d'universelle application tant en pays de plaines qu'en pays de montagnes. Il n'est nécessaire de connaitre ni la position des points de vue, ni l'orientation ou l'inclinaison des plaques, ni la position d'objets communs aux deux vues, excepté pour déterminer l'échelle et la position du plan résultant, ce qui n'offrirait pas de difficulté.†

"Permettez moi de vous signaler une petite erreur typographique à la page 29 the l'extrait de votre livre. Le mémoire du Dr. Pulfrich a été publié dans les numéros 3, 5, 6 et 8 du Zeitschrift für Instrumentenkunde en Mars, Mai, Juin, et Août 1902, non en 1901. Cela n'a d'intérêt que pour montrer que je n'avais pas pu en avoir connaissance quand j'ai présenté en 1901 à la 'South African Philosophical Society' la note (reproduite ensuite dans le journal 'Nature') dont je vous envoie copie avec un extrait des procès-verbaux de la société qui ne peut laisser de doute à ce sujet.

"J'ai fait d'ailleurs emploi de la méthode stéréoscopique en topographie depuis l'année 1898. Je me bornais alors à dessiner le terrain entre points connus et ce fut l'aide remarquable que ce simple procédé me rendit plus d'une fois pour l'analyse des reliefs distants mal définis qui me porta à étudier la question de la mesure de l'image. Dans ce but, après quelques essais dans le sens graphique qui ne m'ont pas satisfait, je fis à l'observatoire

"* Cela est si vrai que, M. Fourcade, s'étant addressé à la Maison Zeiss pour faire construire un appareil réalisant sa conception, il lui a été répondu que cet appareil existait et qu'il pourrait lui être envoyé en communication (renseignement donné par M. le Dr. Pulfrich, qui ne doute pas d'ailleurs qu'il s'agisse simplement d'une coincidence, singulière à coup sur, mais comme il s'en produit cependant assez souvent quand une question nouvelle s'impose à l'attention générale."

† This paragraph refers to methods which will be developed in the following and subsequent papers.

du Cap l'examen de l'appareil qui sert à la mesure des clichés de la carte photographique du ciel. Je dois à cet admirable instrument, conçu par Sir David Gill et exécuté par Repsold, presque toutes les idées que j'ai mises dans mon projet de métrostéréoscope . . . "

Col. Laussedat to H. G. Fourcade, 9th July 1903: " . . . La petite erreur typographique que vous me signalez à propos de la date des publications de M. le Dr. Pulfrich ne peut avoir aucune conséquence fâcheuse. Personne ne mettra en doute l'indépendance de vos idées, leur spontanéité, ce qu'a fait le Dr. Pulfrich tout le premier, comme je l'ai rappelé dans une note. De votre côté, vous ne doutez assurément pas que d'autres avaient pensé à utiliser la stéréoscopie pour faciliter d'abord la reconnaissance plus précise des formes du terrain et enfin pour construire immédiatement les plans sans revenir à la méthode ordinaire des intersections. Je suis convaincu personellement que quatre ou cinq personnes au moins ont été conduites à ce genre de recherches, independamment les unes des autres et j'y vois un indice des plus frappants de la tendence tout à fait naturelle de la nouvelle génération à s'affranchir des lizières dans laquelle les anciennes étaient bien obligées de se laisser lier pour ne pas trébucher.

"Cela dit, je crois avec vous et avec mon excellent ami M. E. Deville que les deux moyens entrevus et même déjà réalisés et expérimentés, appareils micrométriques et appareils graphiques, devront être employés et se prêter un mutuel appui . . . "

Proceedings of the South African Philosophical Society, xiv, pt. 5:

Oct. 2, 1901 (p. xxiii).—" The President [Sir David Gill] briefly summarised Mr. H. G. Fourcade's paper, 'On a Stereoscopic Method of Photographic Surveying,' and intimated that time would be afforded for a demonstration and discussion of the method at the next meeting."

Oct. 30, 1901 (p. xxvi).—" Mr. H .G. Fourcade gave a further explanation and demonstration of his stereoscopic method of photographic surveying, which had been communicated by the President at the close of the last meeting."

" After some discussion of the merits of the plan, it was proposed by Dr. Crawford and seconded by Dr. Flint that the matter of assisting Mr. Fourcade in obtaining financial aid to enable him to have the instrument made which is necessary for his method, should be referred to the Council of the Society. This was unanimously agreed to."

Nov. 27, 1901 (p. xxvii).—" The President stated that the reference to Council with regard to Mr. H. G. Fourcade's instrument for a stereophotographic method of surveying had been favourably received, and the Council had decided to approach the Government regarding financial aid towards the manufacture of the instrument."

April 30, 1902 (p. xxxii).—" The President stated that as the result of his interview with the Right Hon. the Premier to ask for some financial aid to enable the particular phototheodolite described by Mr. Fourcade to the Society at the meeting held on October 2, 1901, to be constructed, he has now received the information that a grant of £200 would be placed at Mr. Fourcade's disposal."

See also " The Observatory," June 1902, p. 238.

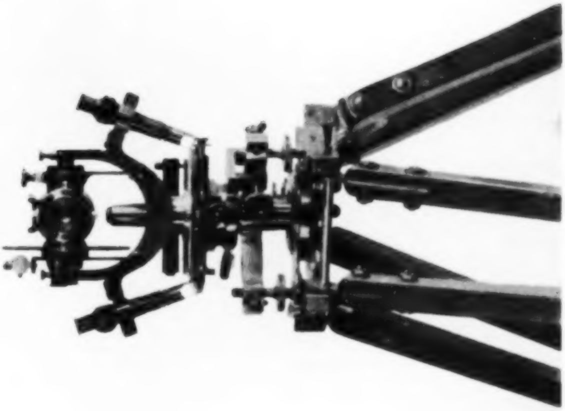

Fig. 2.

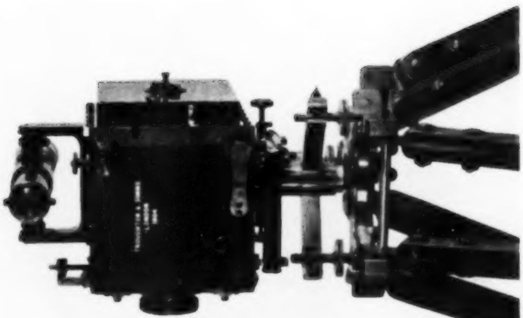

Fig. 1.

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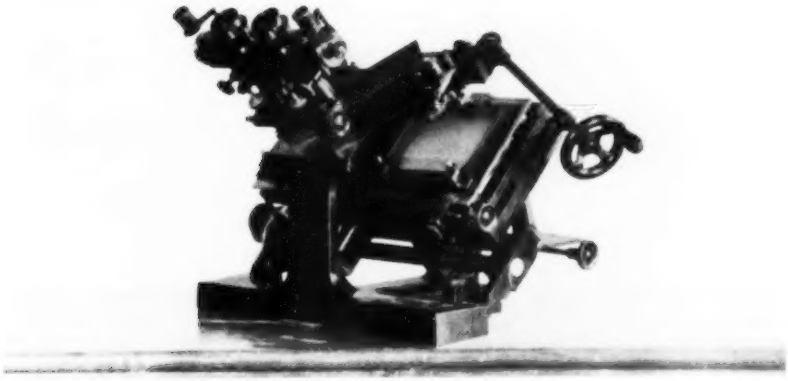

FIG. 1

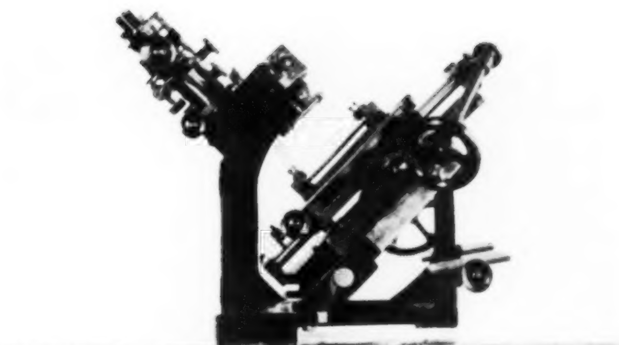

FIG. 2.

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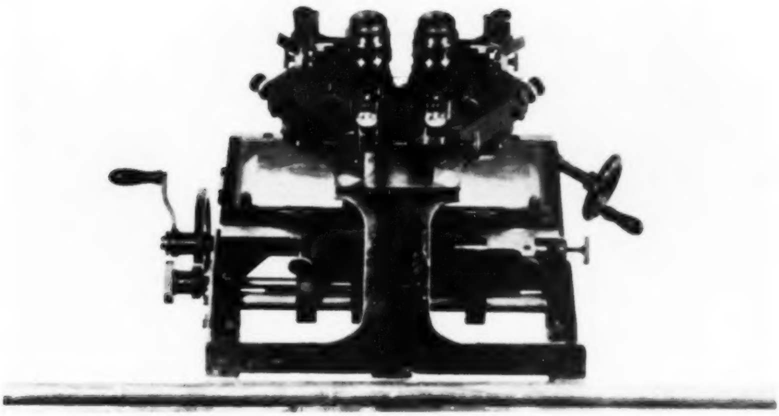

Fig. 1.

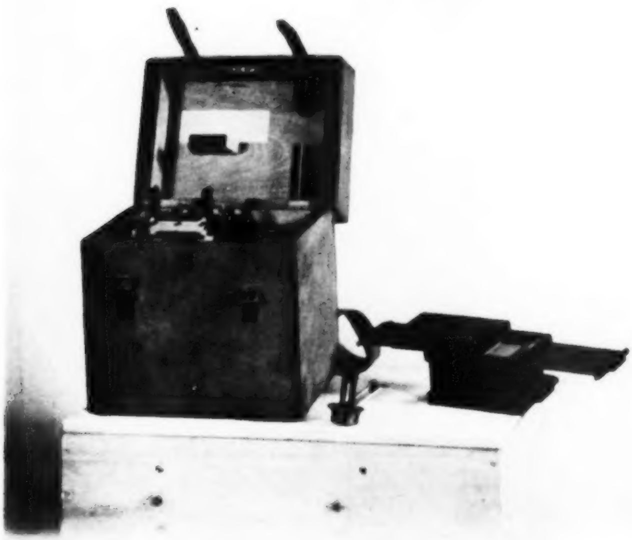

Fig. 2.

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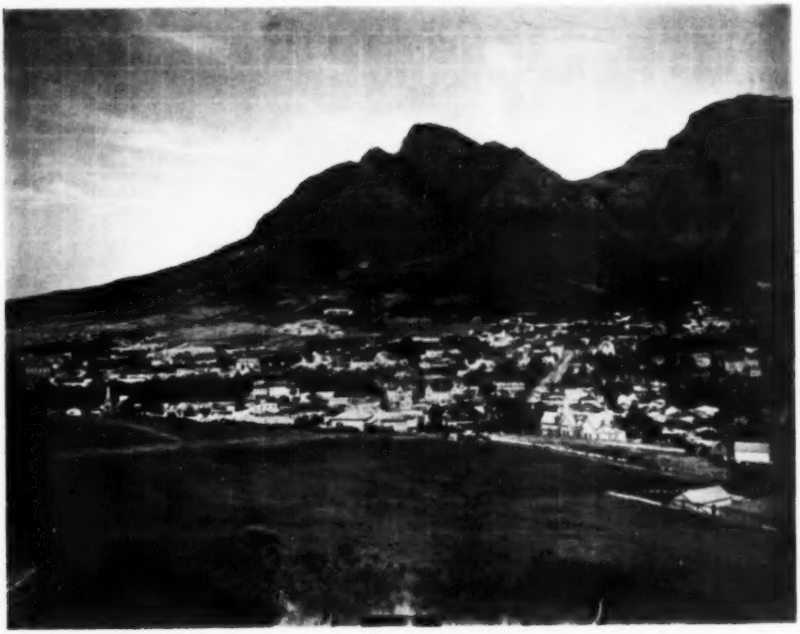

Fig. 1.

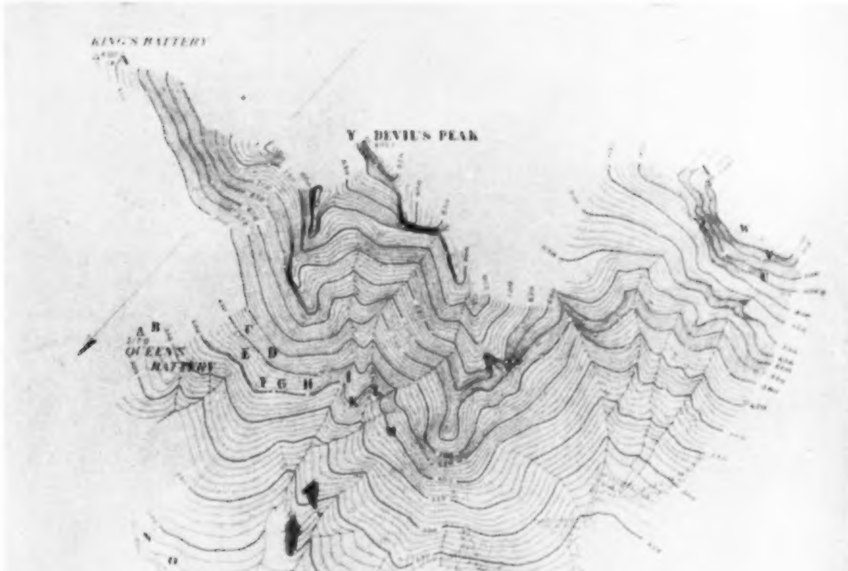

Fig. 2.

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THE OPTICAL TRANSFORMATION OF PROJECTIONS, AND ITS APPLICATION TO MAPPING FROM AIR PHOTOGRAPHS.

By H. G. Fourcade.

(With thirty-one Text-figures.)

Introduction.

In the "Archiv für Photogrammetrie," No. 3 (Nov. 1908), p. 197, R. Thiele mentions that a method of transformation of photographs has been devised by T. Scheimpflug, "Auf mechanisch-photographische wege . . ., weit überflügelnd die bis dato gebrauchliche und schon lange vor der Veröffentlichung Fourcade's praktizierte Verstellung des Neigungswinkel der Platte benig Umphotographieren derselben!"

As a matter of fact, with the exception of a brief allusion by Pulfrich, who states (in the "Zeitschrift für Instrumentenkunde" for Nov. 1903, p. 334) that I mentioned the idea to him, publication of the method of rephotography attributed to me has never hitherto been made.

It appeared to me that my results, or their publication, had been anticipated by Scheimpflug, and for this reason I did not proceed further with the investigation. During the course of a visit to London this year I had for the first time an opportunity of looking up the more recent literature of the subject, notably the publications of Roussilhe * and of the War Office.†

The general treatment of the problem I found to be similar in many respects to my own, but with interesting differences, which induced me to write this paper. What follows may therefore be regarded as consisting in part of a short exposition, from an independent angle, of the present state of the subject, but an exposition practically restricted to what is indispensable for the comprehension of other portions which are believed to remain new. These are, chiefly, the different way in which the equations of optical transformation are established, the extension of the relations connecting conjugate focal surfaces, the generalised graphical solution of

* M. H. Roussilhe, Applications de la photographie aérienne aux levers topographiques de précision, Paris, 1919.

† M. N. MacLeod, Mapping from Air Photographs, London, 1920; and Report of the Air Survey Committee, No. 1, the War Office, London, 1923.

the problem of resection in space, here made applicable to three points at any different heights, the simpler arithmetical solution of the same problem, the elimination of the effect of curvature and refraction in the result, the various mechanical constraints which will give conjugate focal planes, and possibly the interference method of mapping. At the same time brief references are made to other work, and the whole forms a complete and practicable, if still laborious, system of mapping from air photographs.

Further developments in air surveying, introducing new principles which promise to greatly simplify the whole procedure, will be dealt with in succeeding papers, as soon as some experimental instruments which are now being constructed have been sufficiently tested and the details of a working machine finally settled.

Part I.—Optical Transformation of Projections.

1. The means formerly made use of for the transformation of photographic projections were mainly mechanical or graphical, as in Ritter's Perspectograph*, which is a combination of linkages and slides, and the Perspectometer, which is simply a transparent scale of perspective lines.† Dr. Deville has also suggested that when the required "displacement of the camera is too small to affect definition on the screen," transformation may be effected by rephotographing the negative held obliquely to the camera.‡ It was then found, as pointed out by the writer in 1903, and first published in detail by Scheimpflug in 1906, that there is no such limitation, transformation being possible, within a large range, at all angles.

In addition to the direct optical methods, there are others which are partly optical and partly mechanical, as, for instance, by making the exposure through a moving slit and constraining the lens by mechanical means to move in a definite manner relatively to the slit. The panoramic camera and Moessard's Cylindrograph supply examples of this class of transformations, which it is not proposed to consider further because the object can be attained more simply and accurately by a direct method.

2. According to the theory of the equivalent lens, the two principal planes of a lens system may be shown as one in figures, constructions outside their interval remaining the same as if they coincided. For convenience the imaginary common nodal point will be termed the *equivalent centre*, and the imaginary common principal plane *the equivalent plane*. In fig. 1, O may thus be indifferently the first nodal point of a lens with reference

* H. Ritter, Perspektograph, Frankfurt (no date).

† Deville, Photographic Surveying, Ottawa, 1895, p. 88. The appliance is also described by Thiele in No. 1 of the Archiv für Photogr., p. 37.

‡ Deville, *loc. cit.*, p. 227.

to CA, or the second with reference to DB. Let AB be the optical axis of the lens, and CD a ray through O making any angle θ with AB. We have

$$f_1 = \text{OC} \cos\theta$$
$$= \frac{f_1' \sin i_1 \cos\theta}{\sin(i_1 - \theta)},$$
$$f_2 = \text{OD} \cos\theta$$
$$= \frac{f_2' \sin i_2 \cos\theta}{\sin(i_2 - \theta)}.$$

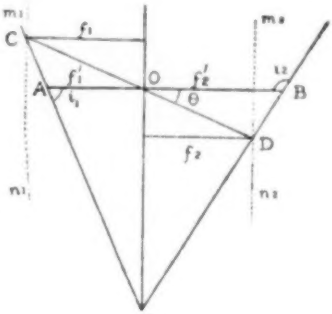

Fig. 1.

When D is the conjugate focus of C and f the focal length of the lens,

$$\frac{1}{f} = \frac{1}{f_1} + \frac{1}{f_2}$$
$$= \frac{1}{f_1'} + \frac{1}{f_2'} - \frac{1}{f_1'}\frac{\tan\theta}{\tan i_1} - \frac{1}{f_2'}\frac{\tan\theta}{\tan i_2}.$$

To make A and B another pair of conjugate foci the last two terms must vanish. The condition then is

$$\frac{\cot i_1}{f_1'} + \frac{\cot i_2}{f_2'} = 0.$$

That is, AC and BD must meet at a point P in the equivalent plane. When i_1 and i_2 are given, the position of P is independent of θ, so that every point of the line PA will have its conjugate focus on the line PC. And, similarly, PA and PB may represent the traces of conjugate focal planes perpendicular to the plane of the figure and intersecting in the equivalent plane. For any point in a line at D perpendicular to the plane of the figure is also contained in a plane m_2n_2, perpendicular to the optical axis, of which the conjugate focal plane m_1n_1 passes through C.

It is therefore possible to reciprocally transform by optical projection through a lens any two plane figures in perspective. The further conditions to be satisfied for lenses of given focus will be investigated later.

The geometrical construction of conjugate focal planes is simple. Let (fig. 2) AC be the trace of one plane and M_1N_1, M_2N_2 the traces of the conjugate focal planes at distances $2f$ from, and parallel to, the equivalent plane OC. From P, where AC intersects M_1N_1, draw the ray PO, meeting M_2N_2 at Q. Q is the conjugate focus of P, and the conjugate focal plane of CP will be CQ, since it must contain Q and pass through C.

To construct the focal length of a lens of which the equivalent centre is at O, and for which CP and CQ are conjugate focal planes, draw OS

parallel to CP and OT parallel to CQ. It is evident that the lengths of the perpendiculars from S or T on CO are equal to the focal length.

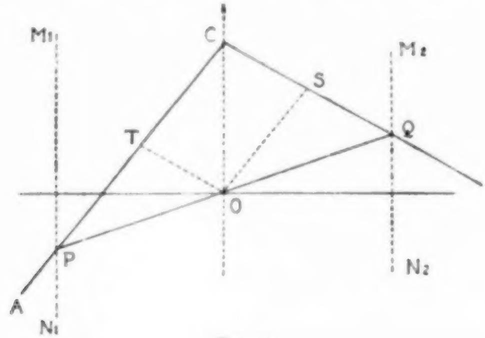

FIG. 2.

Fig. 3 represents particular cases of conjugate focal planes. It is easily seen that, in all cases, the construction corresponds with that of the conjugate rays the conjugate traces might represent. Conjugate rays and conjugate planes have thus correlative relations in conformity with the geometrical principle of duality.* Conjugate focal surfaces are naturally not restricted to planes. The cones generated by the rotation of conjugate

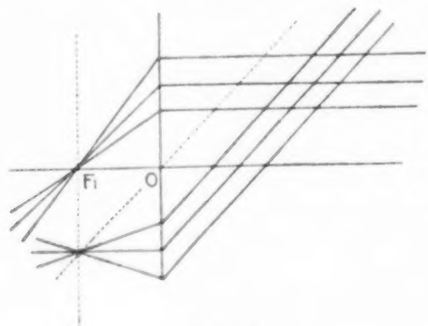

FIG. 3.

rays in an axial plane are conjugate. So are the hyperboloids of one sheet generated by conjugate skew rays. Conjugate focal surfaces are always of the same degree, and the equation of the one may readily be obtained from the equation of the other by substitution of $\frac{fx}{f+x}$, $\frac{fy}{f+x}$, and $\frac{fz}{f+x}$ for

* Staudt, Geometrie der Lage (Nürnberg, 1847), Art. 66.

x, y, and z. Their intersection is always a plane curve in the equivalent plane of the lens.

The method of optical transformation being founded upon the accuracy of the equation $\frac{1}{f_1}+\frac{1}{f_2}=\frac{1}{f}$, it may be useful to notice here that, apart from optical theory, this is a necessary geometrical relation for an ideal lens giving images free of distortion and point pictures of points, conditions approached very closely by modern symmetrical lenses of the best makes when used with a small stop.

A lens free from distortion must have, geometrically, one or two nodal points, these being the respective centres from which the object and the image are in similar perspective. Also, necessarily, principal planes, if a point gives a point image. Let (fig. 4) D be the focal point for rays parallel to the optical axis RD, and EN_1 and CN_2 the traces of the principal planes. A ray AE parallel to the optical axis will pass, after refraction, through D. Draw the ray AN_1 to the first nodal point, and its continuation, after refraction, through the second nodal point N_2 and parallel to N_1A, intersecting CD produced at B, which is the conjugate focus of A. We have then, from the similarity of the triangles N_2CD and HCB,

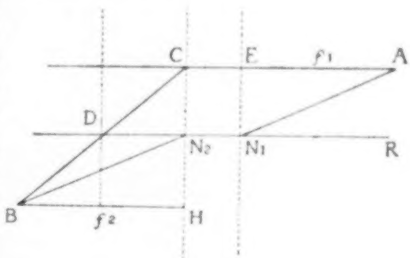

FIG. 4.

$$\frac{h}{f}=\frac{h+x}{f_2},$$

Also from the two similar triangles N_1EA and N_2HB,

$$\frac{x}{f_2}=\frac{h}{f_1}=\frac{h+x}{f_1+f_2},$$

whence

$$\frac{h}{f}=\frac{h(f_1+f_2)}{f_1f_2} \text{ and } \frac{1}{f}=\frac{1}{f_1}+\frac{1}{f_2}.$$

With the usual convention of signs the equation is $\frac{1}{f}=\frac{1}{f_2}-\frac{1}{f_1}$, but the first form is preferred because of the double origin due to the nodal interval.

The equations connecting conjugate focal planes may be put in another form by making $p_1=f_1' \sin i_1$ and $p_2=f_2' \sin i_2$, p_1 and p_2 being the distances of the centre of projection O from the planes of projection PC and PB. p_1 and p_2 are the lengths of the *distance lines* of writers on perspective,

and may be termed more conveniently the *projection distances* of the two perspectives. The equations then become

$$\frac{\cos i_1}{p_1}+\frac{\cos i_2}{p_2}=0,$$

$$\frac{\sin i_1}{p_1}+\frac{\sin i_2}{p_2}=\frac{1}{f}.$$

3. In the relations so far established the projection distances of the two perspectives, and therefore the focal length of the lens used for the transformation, are determinate by the conditions of the problem. A property of figures in perspective will, however, make it possible to extend, within limits, their application to lenses of any other focus.

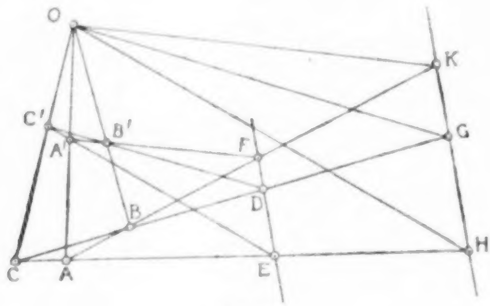

Fig. 5.

Chasles' Theorem. In fig. 5 the points ABC in the plane σ of one plate and A'B'C' in the plane σ' of the other plate are in perspective. FE is the line of intersection of the two planes, O the perspective centre. Through O draw a plane σ'' parallel to the plane σ' and meeting the plane σ in the line HK.

By a theorem in projective geometry,* if the plane σ' be made to turn round $\sigma\sigma'$ the point O will describe a circle, lying in a plane perpendicular to $\sigma\sigma'$ and having its centre upon $\sigma\sigma''$.

Fig. 6 is drawn in the plane which passes through O, and is normal to the planes σ, σ', and σ'', represented by their traces DA, DA_1, and CO_1, so that the angle between the planes σ and σ' is $A_1DA=O_1CA$.

By Chasles' theorem, the projection from O_1 on the plane A_1D of any figure in the plane AC is the same as its projection from O_2 on the plane A_2D, and similar to its projection from O_2 on any other plane parallel to

* Chasles, Géometrie Supérieure (Paris, 1852), Arts. 368, 369. A proposition equivalent to this was also given by Möbius, Barycentrische Calcul (Leipzig, 1827), § 230.

A_2D. The remainder of the figures in this section will be drawn in the same plane, which may be called the normal plane of the transformation.

A corollary may be derived from Chasles' theorem. If two plane figures, A and B, lying in planes σ and σ' are in perspective, and the plane σ is rotated round its vanishing line, the reprojection from the same centre of A on σ' or any plane parallel to σ will always remain similar to B.

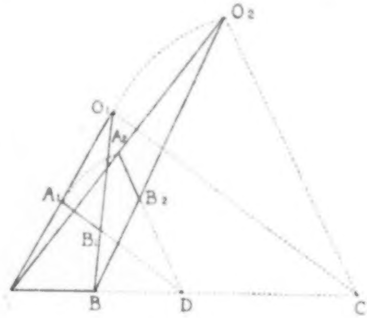

Fig. 6.

For, in the above figure, if the triangle AO_2B be rotated round C until O_2 coincides with O_1, A_2B_2, in perspective with AB, will become parallel to A_1B_1.

4. We can now make use of Chasles' theorem to establish the equations for the general case of optical transformation.

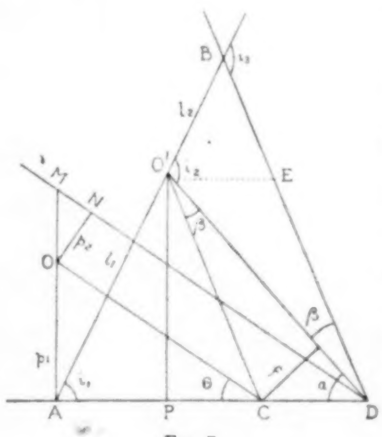

Fig. 7.

In fig. 7 AD represents the plane of a figure required to be projected on any other plane, MD, from any centre of projection O, p_1=OA and p_2=ON being the respective projection distances. Draw OC parallel to MD. If we take a point O′ such that O′C=OC, and draw DB parallel to O′C, the projection of MD, through O, of a figure in AD, will be the same as its projection on BD through O′. If the latter projection is made through a lens with its equivalent centre at O′, it has been shown that O′D will be the equivalent plane of the lens and f=CD sin α its focus. We have, further,

$$CD=\frac{p_2}{\sin\theta},$$

$$\sin\alpha=\frac{f}{CD}=\frac{f\sin\theta}{p_2},$$

$$O'C=OC=\frac{p_1}{\sin\theta}.$$

$$\sin \beta = \frac{f}{O'C} = \frac{f \sin \theta}{p_1},$$

$$O'P = O'C \sin (\alpha+\beta),$$
$$PC = O'C \cos (\alpha+\beta),$$
$$AC = OC \cos \theta = O'C \cos \theta.$$

$$AP = AC - PC = O'C(\cos \theta - \cos (\alpha+\beta)),$$

$$\tan i_1 = \frac{O'P}{AP} = \frac{\sin (\alpha+\beta)}{\cos \theta - \cos (\alpha+\beta)},$$
$$i_2 = \alpha + i_1,$$
$$i_3 = \alpha + \beta + i_1,$$

$$l_1 = \frac{O'P}{\sin i_1} = \frac{p_1 \sin (\alpha+\beta)}{\sin \theta \sin i_1},$$

$$O'D = \frac{O'P}{\sin \alpha} = \frac{p_1 \sin (\alpha+\beta)}{\sin \theta \sin \alpha},$$

$$l_2 = \frac{O'D \sin \beta}{\sin i_3} = \frac{p_1 \sin (\alpha+\beta) \sin \beta}{\sin \theta \sin \alpha \sin i_3}.$$

But

$$p_1 \sin \beta = p_2 \sin \alpha,$$

so that

$$l_2 = \frac{p_2 \sin (\alpha+\beta)}{\sin \theta \sin i_3}.$$

Collecting these results we have :

$$\sin \alpha = \frac{f \sin \theta}{p_2},$$

$$\sin \beta = \frac{f \sin \theta}{p_1},$$

$$\tan i_1 = \frac{\sin (\alpha+\beta)}{\cos \theta - \cos (\alpha+\beta)},$$

$$i_2 = \alpha + i_1,$$
$$i_3 = \alpha + \beta + i_1.$$

$$l_1 = \frac{p_1 \sin (\alpha+\beta)}{\sin \theta \sin i_1},$$

$$l_2 = \frac{p_2 \sin (\alpha+\beta)}{\sin \theta \sin i_3}.$$

If the projection required is that which would have been taken from the same point with the same camera at an inclination differing by the angle of transformation θ, as when it is wanted to transform an aerial negative taken with a tilted camera into its projection on a horizontal

plate with the same projection distance, and the reprojection is made through the camera lens, the relations become simpler. We have then

$$p_1=p_2=f,$$
$$\alpha=\beta=\theta,$$
$$\tan i_1=\frac{\sin 2\theta}{\cos\theta-\cos 2\theta},$$
$$i_2=i_1+\theta,$$
$$i_3=i_1+2\theta,$$
$$l_1=\frac{2f\cos\theta}{\sin i_1},$$
$$l_2=\frac{2f\cos\theta}{\sin i_3}.$$

Again, using for the reprojection a lens of focal length f shorter than p_1 the focal length of the camera lens, l_1 may be made equal to p_1 when the relations become simpler still. We get in this case,

$$i_1=90^\circ,$$
$$\sin\beta=\frac{f}{p_1}\sin\theta,$$
$$\alpha=\theta-\beta,$$
$$l_2=\frac{f\tan\theta}{\sin\alpha},$$

but we are restricted to the condition

$$p_2=\frac{f\sin\theta}{\sin\alpha}.$$

In certain cases this method has advantages, but it is limited to small angles of transformation because the axis of projection makes with the optical axis a greater angle than in the other methods.

The positions of the plates may also be given with reference to the optical axis of the lens (SR in fig. 8). The relations then become

$$\sin\beta=\frac{f\sin\theta}{p_1},$$
$$\sin\alpha=\frac{f\sin\theta}{p_2},$$
$$f_1=f\left(1+\frac{\tan\alpha}{\tan\beta}\right)=\frac{\sin(\alpha+\beta)}{\cos\alpha\sin\beta},$$
$$f_2=f\left(1+\frac{\tan\beta}{\tan\alpha}\right)=\frac{\sin(\alpha+\beta)}{\sin\alpha\cos\beta},$$
$$d_1=\frac{p_1}{\sin\theta}\left(\frac{\cos\beta}{\cos\alpha}-\cos\theta\right),$$

$$d_2 = \frac{p_2}{\sin\theta}\left(\frac{1}{\cos\theta} - \frac{\cos\alpha}{\cos\beta}\right),$$

$$i_1 = 90^\circ - \alpha,$$
$$i_3 = 90^\circ + \beta;$$

reducing for the case of $p_2 = p_1 = f$ to

$$\alpha = \beta = \theta,$$
$$i_1 = 90^\circ - \theta,$$
$$i_2 = 90^\circ + \theta,$$
$$f_1 = f_2 = 2f,$$

$$d_1 = p_1 \sin\frac{\theta}{2},$$

$$d_2 = \frac{p_2}{\cos\theta}\sin\frac{\theta}{2}.$$

Correction for Nodal Points.—When the positions are referred to the optical axis, l_1 and l_2 (fig. 8) have simply to be reckoned from the corresponding nodal points.

When the positions are referred to the line from the centre of projection to the centre of the plate, if the lens is pivoted at its first nodal point, l_1, α, β, i_1, i_2, i_3 (fig. 7) remain unchanged, but l_2 must be reckoned from a point at a distance from the first nodal point equal to $\dfrac{d\cos\beta}{\sin i_3}$, d being the distance apart of the two nodal points.

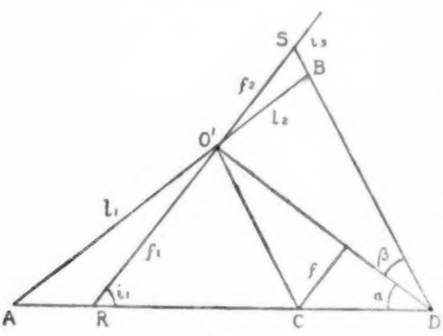

FIG. 8.

5. *Design of Projection Camera.*—Two constructions are possible, according as to whether we choose to refer the settings to the optical axis, or to the axis from the centre of the lens to the centre of the plate to be projected. In the first case the computations for the settings are a little simpler, but the mechanical construction of the apparatus is more complicated. In the other case we require only one longitudinal slide for varying the distances of the plates from the lens and three axes for the rotations of the two plates and that of the lens, instead of two axes and three slides, the relative position of which it is difficult to keep mechanically accurate. In both cases the plates must be capable of rotation in their own planes about

their respective centres, and means must be provided for centering the negative to be projected. To allow of settings being made from zeros given by spirit-levels, it is more convenient to make the rotation axes horizontal than to make them vertical.

Fig. 9 represents the frame for holding the negative and part of the slide. The slide is made of three steel straight edges mounted on a base board, not shown. A and B are fixed with the longer side of their sections vertical, and C with the longer side horizontal. This arrangement makes flexure of the straight edges from their thinness to be of no significance, while giving great rigidity to the effective guiding surfaces. To ensure the guiding surfaces of A and B being accurately in one plane, A or B may be fixed to the base by a pin at one end and adjusted by means of a screw at the other end until a spirit-level remains horizontal when laid across either end of the slide. The supporting stand DD of the frame F has three contacts, *a b c*, in the plane of its base, and two contacts, *d e*, in a vertical plane against the respective guiding surfaces of the straight edges, the whole forming a well-conditioned "geometrical slide." Two opposing flat springs serve to maintain the horizontal and the vertical contacts. Divided scales fixed to C and verniers carried by the sliding arms serve to measure the distances of the centres of the plates from the nodal points of the lens.

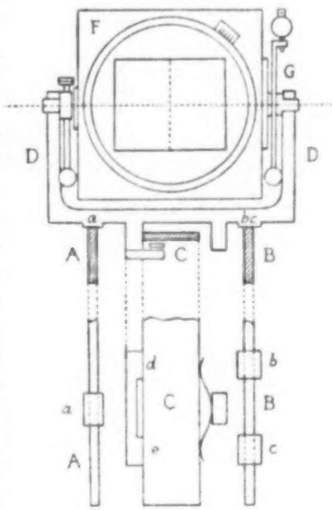

Fig. 9.

The inclination of the frame F is measured by a small vertical circle at G, with a spirit-level mounted on its vernier plate after the manner of a theodolite circle, and likewise provided with screws and a clamp.

The frames and stands for the lens and for the second plate are similar, except that for the lens the stand remains fixed and its frame does not rotate, and, for the second plate, that the rotating circle of the frame need not be graduated.

Extraneous light is excluded by means of bellows between the frames and a cover over the sensitive plate.

The exposures may be made with a lantern, but it was found in the case of a copying-camera, constructed for the author by Messrs. Troughton & Simms in 1903, that they could be made quite satisfactorily with daylight

diffused through a ground-glass screen carried in front of the negative. In this camera there were no dark slides, both negative and sensitive plate being held by springs pressing against three stops corresponding to stops in the author's surveying camera described in the B.A. Reports for 1905. The procedure was to insert a plate in the camera in the dark room, replace the cover at the back of the sensitive plate, take the camera to a window and give a time exposure with a shutter consisting of a flap worked by a button outside the camera. Lantern plates were used and gave very clear reprojections.

PART II.—DETERMINATION OF THE RELATIVE POSITION OF TWO FIGURES IN PERSPECTIVE.

Before we can transform an air photograph into the projection, on a horizontal plane, of the same view from the same point of view, we require to determine the inclination of the plate, and the direction on the plate of this inclination. And, to make use of the reprojection for mapping, we require, further, to find its orientation and the position in space of the view-point. To effect these determinations, it is theoretically sufficient, if we have the focal length of the camera lens and the position of the plate centre, to know the position on the ground of three points shown on the photograph.

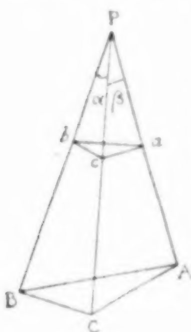

FIG. 10.

We may obtain the results by graphical construction, by computation, or by optical means. These three methods will be considered in turn.

Let *abc* (fig. 10) represent three points on the photograph, and ABC the three corresponding points on the ground. The two triangles *abc*, ABC being in perspective, their corresponding sides will subtend the same angles α, β, γ from the perspective centre P.

To construct these angles plot (fig. 11) the plate co-ordinates of *abc* on any suitable scale. Join the origin O, which is the plate centre, to *a*, *b*, and *c*. Having O*a*, O*b*, and O*c*, the triangles PO*a*, PO*b*, and PO*c*, right-angled at O (fig. 12), and in which PO is made equal to the focal length, will give the distances P*a*, P*b*, P*c* of the projection point from *a*, *b*, and *c*. And the triangles P*ab*, P*ac*, and P*bc*, in which all the sides are now known, will give the angles $\gamma = a\mathrm{P}b$, $\beta = a\mathrm{P}c$, and $\alpha = b\mathrm{P}c$. Having α, β, and γ, the next

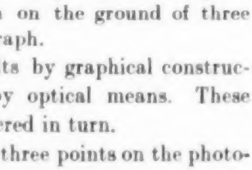

FIG. 11.

step is to construct PA, PB, PC. In fig. 13, if AB, AC_1, and BC_2 are the lengths, on any other suitable scale of the sides of the triangle ABC

Fig. 12.

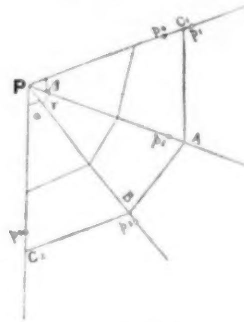

Fig. 13.

and $PC_1 = PC_2$ the distances, PA, PB, PC are determined. But the construction can only be effected by successive approximation. Starting, by estimate, from a point p_1 on PC_1 and drawing successively with radii C_1A, AB, and BC_2 arcs intersecting PA, PB, PC_2 at p_2, p_3, and p_4 we obtain on PC_2 a distance Pp_4, which is different from Pp_1 unless p_1 coincides with C. Another point must therefore be tried, and the process repeated until p_1 and p_4 are made to coincide.*

In fig. 14 ABC is the ground triangle, and since $AP_1 = AP_3$, $BP_1 = BP_2$ and $CP_2 = CP_3$ are known from the construction of fig. 13, the sides P_1BA, P_2CB, and P_3CA of the pyramid PABC, developed about ABC, may be constructed by intersections. From $P_1P_2P_3$ draw perpendiculars to the corresponding sides of ABC, meeting at Q, which is the foot of the perpendicular from P on ABC. To find the length PQ of this perpendicular, join Q to one of the triangle points A, and construct the triangle PQA, right-angled at Q and with $AP = AP_3$. We have now determined the elements of the pyramid, but with reference to the plane of the basal triangle, which may not be horizontal.

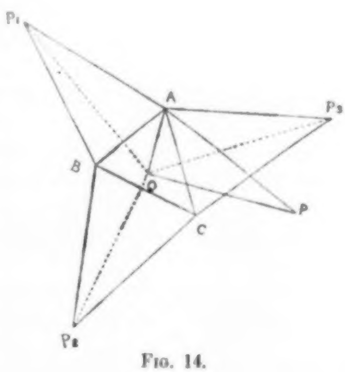

Fig. 14.

In this case the basal triangle will first have been derived from its orthogonal

* This is now known as Hugershoff's "Pyramid Construction."

horizontal projection, which is the map triangle, by the construction shown in fig. 15, where A_1B_1C is the map triangle as plotted from the co-ordinates of its points, and AB, BC, CA the lengths of the sides of the ground triangle, obtained by making B_1B perpendicular to B_1A_1 and to B_1C, equal to the difference in height between B and C, and A_1A perpendicular to the sides A_1B_1, and A_1C equal to the difference in height of A and C.

Draw RT parallel to B_1C at a distance equal to A_1A, and MN perpendicular to B_1C. Join A_1N. The line AM will, in space, be horizontal, since A and M are at equal heights above the horizontal datum plane A_1B_1C. A_1N will be the direction of that line, and CD parallel to A_1N will be the intersection of the planes of ABC and A_1B_1C. Draw (fig. 16) from A_1 and B_1 perpendiculars A_1D and B_1E on CD. A and B being in

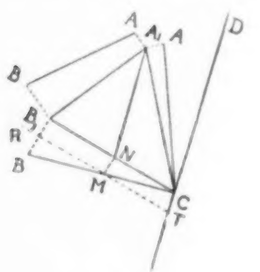

FIG. 15.

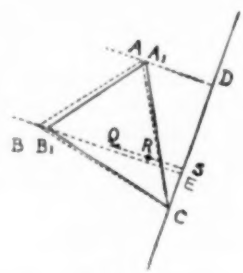

FIG. 16.

the vertical planes of A_1D and B_1E, if we rotate ABC about CD until the planes of ABC and A_1B_1C coincide, A and B will lie respectively on the lines A_1D and B_1E produced. From C draw an arc with radius CB intersecting EB_1 produced at B, and another arc with radius CA intersecting DA produced at A. This will give ABC in its position relatively to CD. The construction will be better if the least acute intersection is alone used for A or B, and the other point determined by intersection with radius BA.

Transfer now on ABC Q derived from fig. 14, and draw QS perpendicular to CD.

In fig. 17 draw the triangle AA_1D, right-angled at A_1 and known from figs. 15 and 16. Make QD equal to QS from fig. 16, and draw PQ perpendicular to QD. The length of PQ is known from fig. 14. From P draw a perpendicular PR on A_1D. PR will be the height of the projection point above the datum plane, and RD the distance between CD of fig. 16 and the vertical of P. Transfer to fig. 16 R by making RS along SQ equal to RD.

In the next figure (fig. 18) A_1B_1C and R are as in fig. 16. Join RA_1 and RB_1, and draw perpendiculars A_1A and B_1B equal to the respective heights of A and B above C, and the perpendicular PR equal to PR of

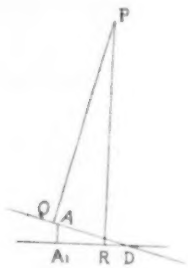

FIG. 17.

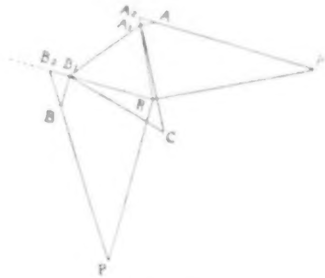

FIG. 18.

fig. 17. The intersection at A_2 of lines through P and A and R and A_1 will be the projection from P of A on the datum plane, and similarly B_2 will be the projection of B.

In fig. 19 *abc* represents the plate triangle, and A_2B_2C the datum triangle, and LN is the intersection of their planes. OG and RG are perpendiculars

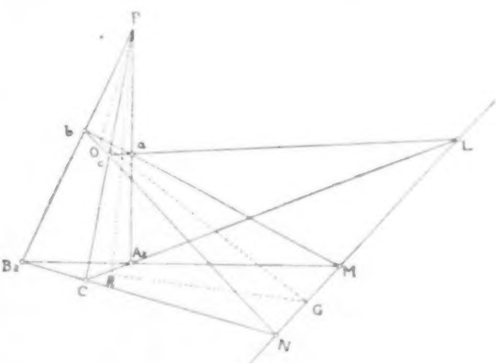

FIG. 19

on LN from O and R. Since the plane of POG is perpendicular to the plane of *abc*, and the plane of PRG is perpendicular to the plane of A_2B_2C, and both are perpendicular to LN and contain P, the perpendiculars meet at G and the figure POGR lies in a plane. The inclination of the plate *abc* will be given by the angle OGR, and its direction by the line OG. In order

to get these, first reconstruct (fig. 20) the pyramid, having the datum triangle for base and PR for height, proceeding as in fig. 14.

Then on the developed sides plot (fig. 21) the sides of the triangle *abc*,

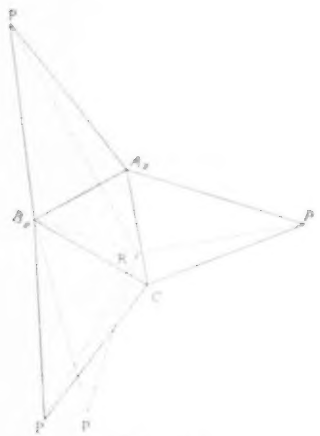

Fig. 20.

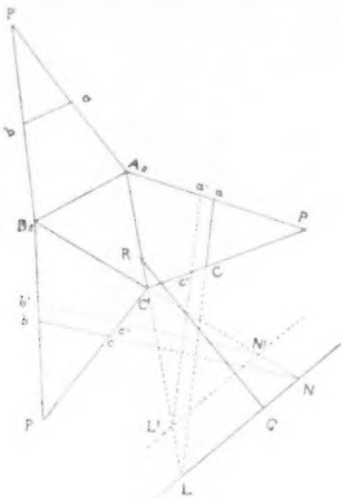

Fig. 21.

using any suitable scale (as either *ac* or *a'c'*). Produce *ac* and A_2C meeting at L, and *bc* and B_2C meeting at N. Join LN, and draw RG perpendicular to LN. It will be seen by comparing figs. 19 and 21 that LN is the direction of the horizontal in the plane of the plate. Draw (fig. 22) PR, obtained from fig. 20, perpendicular to RG, and with radius *f* on the scale that was taken for *abc* draw an arc to which make GO tangent. The angle OGR gives the inclination θ of the plate, the direction of which is still required to be determined. Produce (fig. 24) the sides *ac* and *bc* of the plate triangle, and transfer the lengths *c*L and *c*N from fig. 21. Join LN, which is the direction of the horizontal on the plate and completes the determination of the constants, which are required to be known for reprojecting the plate on a horizontal, or any other, plane.

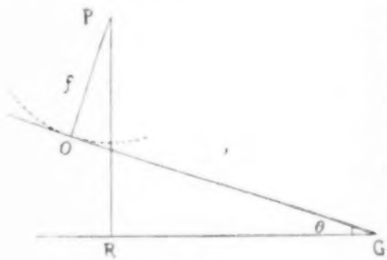

Fig. 22.

It is convenient to make the plate scale an exact multiple of the map scale, so that lengths may be readily transferred from the one to the other.

Although the constructions have been separated for clearness, they may all be done on the two triangles plotted from the plate co-ordinates and the map co-ordinates, rubbing out, if necessary, to avoid confusion, intermediate constructions once they have served their purpose.

Determination of Constants by Computation.

The graphical constructions which have been described can be followed, step by step, by equivalent computations.

A. *Plate Pyramid.*—Let x_a, y_a, etc., be the plate co-ordinates, s_a, s_b, s_c the sides of the plate triangle, l_a, l_b, l_c the edges of the pyramid, and α, β, γ the vertex angles. We have

$$s_a^2=(y_c-y_b)^2+(x_c-x_b)^2,$$
$$l_a^2=x_a^2+y_a^2+f^2,$$
$$\cos\alpha=(l_b^2+l_c^2-s_a^2)/2l_bl_c,$$

and similarly for s_b, l_b, β and s_c, l_c, γ.

The computations are readily done with the help of Barlow's tables. If four significant figures are not considered sufficient, differences obtained at sight or with a slide rule from the relation $(a+\triangle a)^2=a^2+2a\triangle a$, where $\triangle a$ are additional decimals, may be used.

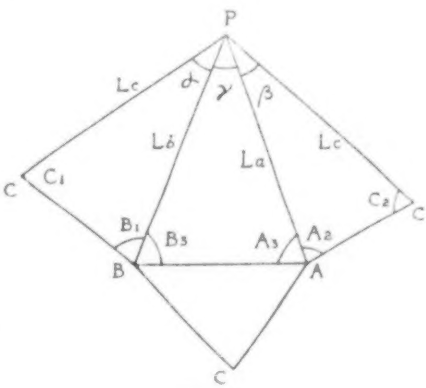

FIG. 23.

B. *Ground Pyramid.*—We can easily get three equations determining the basal angles, but they are in an implicit form which does not admit of ready solution. By differentiating them we obtain three linear equations, connecting the corrections, and these can be solved, using the approximate values of the angles obtained graphically.

A simpler procedure is to start from an approximate value, given by the graphical construction, of the length of one of the pyramid edges, L_c. Then (fig. 23)

$$\sin A_2=\frac{L_c\sin\beta}{b},\quad C_2=\pi-\beta-A_2,$$

$$L_a=\frac{b\sin C_2}{\sin\beta},$$

$$\sin B_3=\frac{L_a\sin\gamma}{c},\quad A_3=\pi-B_3-\gamma,$$

$$L_b=\frac{c\sin A_3}{\sin\gamma},$$

$$\sin C_1=\frac{L_b\sin\alpha}{a},\quad B_1=\pi-C_1-\alpha,$$

$$L_c=\frac{a\sin B_1}{\sin\alpha}.$$

Recompute with the mean of the two values of L_c, which should be very nearly correct, if the initial value was sufficiently close to make second differences negligible throughout. If not, a second mean is taken.*

C. *Computation of Datum Triangle.*—The second pyramid was supposed to be referred to the ground triangle, but it will save a double computation if we proceed first to the determination of the datum triangle and use this instead. We start again from approximate values, obtained from the construction of fig. 20, of PR and of the co-ordinates of R. The co-ordinates of A_2 and B_2 may then be computed from $RA_2=RA_1+A_1A_2$ and $RB_2=RB_1+B_1B_2$, A_1A_2 and B_1B_2 being given by

$$A_1A_2=\frac{RA_1(h_a-h_c)}{PR-h_a+h_c},$$

$$B_1B_2=\frac{RB_1(h_b-h_c)}{PR-h_b+h_c}.$$

Supposing PR = 10,000 feet, $h_a-h_c=100$ feet, $RA_1=3000$ feet, a m. sq. error of 1/500 in PR and RA_1 would give an error of $\sqrt{2}/500$ in A_1A_2; that is, of only one inch for $A_1A_2=30$ feet.

D. *Co-ordinates of Air Station.*—In fig. 14 we can compute the triangle P_1AP_3, of which we know two sides, and the contained angle $P_1AP_3=A_1+A_2+A_3$, and the co-ordinates of Q, which is the foot of the vertical of the air station, from the triangle QP_1P_3, of which we now know the base P_1P_3 and the two adjacent angles. The height PQ of the air station is then found from the right-angled triangle PAQ, in which we know AP and AQ.

E. *Horizontal of Plate.*—In fig. 21, $Pb=\frac{l_b\times Pa}{l_a}$, and in triangle Pbc

$$\sin b=\frac{l_c\sin a}{s_a},$$

* [A similar method of computation was given by S. Finsterwalder in the "Jahresbericht der deutschen Mathematikervereinigung," vol. vi (1897), 2. H. G. F., Sept. 1926.]

so that we can compute the two sides of the triangle NbB_2 and the co-ordinates of N. Similarly the co-ordinates of L may be computed from the triangle LaA_2. LN will then be the direction of the horizontal on the plate.

F. *Tilt of Plate.*—In the triangle RNG (fig. 21), RG = RN sin N, and in triangle PRG (fig. 22)

$$\tan G = \frac{PR}{RG}; \; PG = \frac{PR}{\sin G},$$

and

$$\sin (G - \theta) = f/PG,$$

determining θ, the inclination of the plate.

G. *Orientation of the Plate.*—In fig. 24 compute the plate co-ordinates

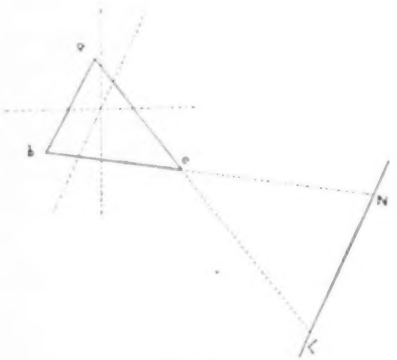

FIG. 24.

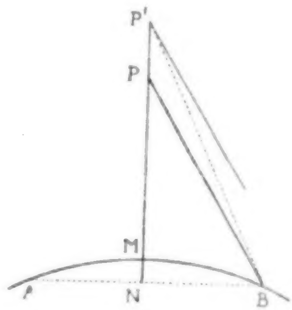

FIG. 25.

of L and N from aL and bN, which are known (fig. 21). Then LN is the direction of the horizontal referred to the plate axes, this completing the solution.

H. *Curvature and Refraction.*—Corrections for curvature and refraction are best disregarded when making use of plates of which the inclination is small.

The computed position of P is not its true position at P′ (fig. 25), but its apparent position at P obtained by ignoring the refraction of the rays to A, B, and C. From the constants, A, B, and C will be reproduced correctly without reference to curvature and refraction, and for other points on the plate the maximum error at MN will not exceed $h = \frac{x^2}{2R}$, where h = MN, x = NB, and R is the radius of the earth. Suppose AB = 3000′ and MP′ = 10,000′, h = 0·21 foot, which is negligible.

Indeterminate Cases.—In ordinary surveying the position of an unknown point cannot be determined from the angles subtended by three known points if the four points lie on a circle. Similarly, with resection in space, the problem becomes indeterminate when the air station is on the surface of the cylinder of which the base is the circle circumscribing the three ground points.

Other Computation Methods.—Other methods of computation have been devised by Finsterwalder,* Hugershoff,† and Fischer,‡ the last modified by Eggert.§ They all depend on a first approximation obtained otherwise, and have another common feature in being exceedingly laborious, as may be imagined from the circumstance that, by Hugershoff's method, it takes twenty hours to compute the constants for a pair of plates, even after having used an instrument called a "photogoniometer" to measure the apex angles directly instead of computing them. Latterly Hugershoff has sought, by making increased use of mechanical means, to reduce the time required for the computations. But it is unlikely that any of these complicated methods will ever come into general use, and, apart from this, their consideration is foreign to the object of this paper.

An interesting method, applicable to four fixed points nearly in one plane, is given in detail in the Report of the Air Survey Committee, 1923, p. 100.

Instrumental Methods.—An instrument called a "Tilt-finder," devised by Col. MacLeod, is described in the Report of the Air Survey Committee, 1923, p. 24. It is designed for the setting in perspective of a photograph and a frame carrying markers which can be adjusted to correspond, on a proper scale, to the relative position in space of the ground points. The eye-hole is at a distance from the photograph, equal to the focal length of the lens it was taken with, multiplied by the ratio of the enlargement. When, by trial and error conducted in a systematic manner, the corresponding points on the photograph and on the frame have been made collinear with the eye-hole, the photograph and the ground points are in their correct relative positions, whence the constants for the plates can be read on the scales of the apparatus or measured otherwise. This instrument promises to be of considerable value, either for a sufficient determination of the plate constants, or, at any rate, to obtain first approximations, which may dispense with the necessity of using graphical constructions.

* Finsterwalder, S., Eine neue Lösung der Grundaufgabe der Luftphotogrammetrie, Proc. of the Bavarian Ac. of Sc., Munich, 1915.

† Hugershoff, R. and Cranz, H., Grundlagen der Photogrammetrie aus Luftfahrzeugen, Stuttgart, K. Wittwer, 1919.

‡ Fischer, T., Ueber die Berechnung der raumlichen Rückwartseinschnitt bei Aufnahmen aus Luftfahrzeugen, Jena, G. Fischer, 1921.

§ Eggert, O., Rückwartschneiden im Raum, Zeitsch. f. Verm., 49, pp. 9, 273, 1920.

Camera Lucida.—A camera lucida may similarly be used to set two figures in perspective, but in practice the adjustment is found to be slow and difficult, and there are other drawbacks regarding parallax and the relative illumination of the photograph and the map, so that attempts that have been made to bring the instrument into use have generally been abandoned.*

Adjustment with Projection Camera.—If the negative is placed in its holder and a plotted figure of the ground triangle in the opposite holder, it is theoretically possible, but practically difficult, to make the projected images of the plotted points coincide with their positions on the plate. The difficulty of the operation is due to the circumstance that there are seven separate adjustments to be made, namely: (1) Rotation of negative, (2) Rotation of positive (plotted triangle), (3) Inclination of negative, (4) Inclination of positive, (5) Cant of lens, (6) Distance of negative, (7) Distance of positive—and that change in any one of these variables will generally upset any adjustment made for the others. Experimenting with the camera of 1903, the author found it very tedious to obtain coincidence, and concluded that the method could not readily be made to yield practical results.

The method was first proposed by Scheimpflug † in 1906. More recently, by developing a definite system of procedure, and the use of graphs constructed from the transformation equations, Roussilhe ‡ has succeeded in reducing the time required for the adjustment and the subsequent transformation to 25 minutes. When the height of the aeroplane is between 1500 and 2500 m. the tilt can be determined within 30′ of arc, and the co-ordinates of the air station within 10 m. The modified method, being comparatively simple and expeditious, promises to become of permanent value for the mapping of flat country, but its utility for hilly ground is more limited.

It is also possible to introduce mechanical constraints which will reproduce the relations between the variables given by the transformation equations and, by reducing the number of variables to be dealt with, render the adjustment more manageable.

Scheimpflug was the first to use a mechanical arrangement for the purpose, based on the geometrical construction of fig. 2. Let (fig. 26) AB be the optical axis of the lens, O its equivalent centre, OC the equivalent

* Report of the Air Survey Committee, 1923, p. 38. See also Mapping from Air Photographs, 1920, p. 17.

† Scheimpflug, Th., "Der Perspektograph und Siene Anwendung," Photographische Korrespondenz, 1906.

‡ Roussilhe, H., *loc. cit.*, 1917, Comptes rendus, 175, 21, 949 (1922), and La Géographie, 38.1.1. (1922).

plane, m_1n_1, m_2n_2 the principal focal planes, M_1N_1, M_2N_2 the two focal planes for magnification 1, at distances $2f$ from the equivalent plane, and CP, CQ two conjugate focal planes intersecting the optical axis at A and B in the planes M_1N_1 and M_2N_2. If we move O to O′ while keeping TT′ = OO′ and BB′ = 2TT′, B′T′ will remain continuously conjugate with CA. Similarly if we keep CB or CB′ fixed and impart the same corresponding motions to O, S, and A we can alter the angle α while keeping CA conjugate with CB or CB′. The motions along the parallel slides M_2N_2 and m_2n_2 and OC are imparted by screws of equal pitch, connected by gearing which gives two revolutions to the screw along M_2N_2 for each revolution of the screw at m_2n_2. There is another pair of screws, similarly geared, for m_1n_1 and

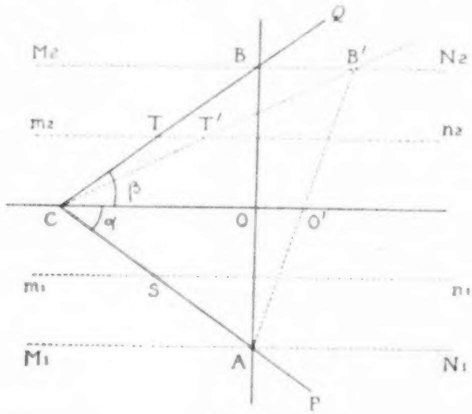

FIG. 26.

M_1N_1, and O can be connected to move either with T or with S. By making the distance between the two planes of magnification 1 equal to $4f+s$ and the distance between the two principal focal planes equal to $2f+s$, the effect of the nodal interval s is eliminated.

In order to keep the slides horizontal, the plates, in Scheimpflug's camera, are made to tilt about vertical axes.

Since S and A must remain in their corresponding slides, it is obvious that the angles α or β cannot be made very small, so that the transformation is limited to inclined plates.

A number of other movements were designed by the present writer. While keeping the plates in conjugate planes it is possible to make the scale of the projection vary continuously without changing its shape, and to introduce further conditions, but the complication of the movement increases with the number of conditions it must satisfy.

One of the simpler forms, in which the limitation of Scheimpflug's apparatus to inclined plates is removed, may be noticed here:

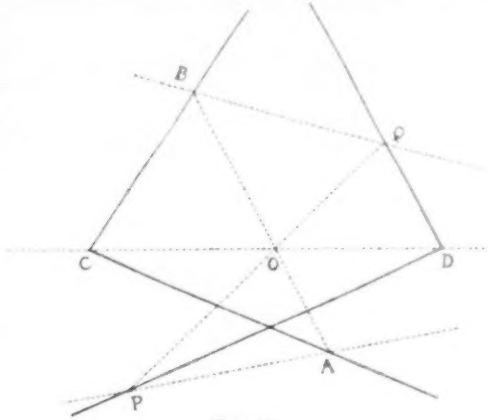

FIG. 27.

CA, CB and DP, DQ (fig. 27) are any two pairs of conjugate planes with centres at O. If we make BOA collinear in the first pair and POQ collinear in the second pair, then AP and BQ are also a pair of conjugate planes. By increasing the distance between the two upper and the two lower slides in the figure by *s*, reckoned perpendicularly to CD, the effect of the nodal interval is eliminated. The position of A and P on the fixed slides AC and PD being arbitrary, AP may be any plane within the range of the apparatus.

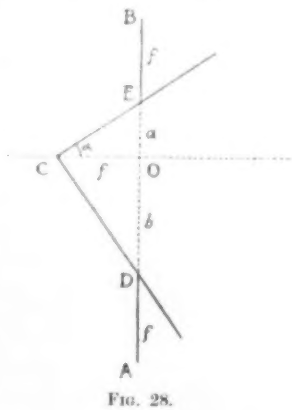

FIG. 28.

The correspondence of conjugate points may be achieved in other ways. For instance, two points along the optical axis may be constrained to remain conjugate by the following construction: ECD is a rocking piece with two arms, CE and CD, at right angles, pivoted at C in the equivalent plane at a distance f from O. AD and BE are two distance pieces, of length f, sliding along the optical axis. Then

$$\frac{1}{a+f}+\frac{1}{b+f}=\frac{1}{f+f\tan\alpha}+\frac{1}{f+f\cot\alpha}=\frac{1}{f},$$

so that B always remains the conjugate focus of A. Here again AD and

BE should be made equal to $f+\frac{s}{2}$ on account of the nodal interval. This construction was suggested by an example in Salmon's Conic Sections.*

Another method of connecting conjugate foci along the optical axis would be to use a parabolic cam. The polar equation is

$$\rho=\frac{p}{1+\cos\omega}.$$

Make $p=2f$, then if ρ_2 is the radius vector 180° from ρ_1,

$$\frac{1}{\rho_1}+\frac{1}{\rho_2}=\frac{1+\cos\omega}{2f}+\frac{1+\cos(\pi+\omega)}{2f}=\frac{1}{f}.$$

By making $\rho=\frac{p}{1+\cos m\omega}-C$ the construction would be better conditioned mechanically, but the range of ρ reduced.

It is unlikely, however, that the aid afforded by mechanical devices will compensate for the loss of accuracy which their complication introduces. Another drawback is that to convert the ground triangle into its projection on a datum plane, graphical constructions will still be necessary. If it is possible to make these sufficient there could be no object in going further. Much could be done to increase the accuracy of graphical constructions by drawing diagrams on a large scale, making use of drawing instruments comparable in point of precision to engineer's fine gauges, and substituting computations wherever they are simple. To avoid error from expansion of the paper through absorbing moisture, the sheet would have to be first damped and then glued by its edges to a drawing-board of varnished wood, so as to remain in tension under all ordinary conditions of atmospheric humidity.

Part III.—Mapping from Air Photographs.

The inclination and orientation of the plates being known, they can be transformed in the projection camera into projections on any other planes containing the respective air stations. The planes chosen may be either (*a*) the two horizontal planes through the stations, (*b*) a plane containing the base and the horizontal lines perpendicular to the base.

In the first case, the map may be constructed by the usual intersection methods of photographic surveying. Either picture forms already an approximate map, and constructions will be required only to supply a sufficient number of reference points serving to interpolate the remainder of the map. On level ground no correction is needed beyond a change of scale.

Interference Method.—Another procedure may consist of the superposition on the map of projections from the two negatives.

* G. Salmon, Conic Sections, ed. 1879, p. 48.

In fig. 29 let, on the scale of the map, A and B be the two air stations, m_1n_1, m_2n_2 the two negatives corrected for tilt, and CD the datum plane on the ground. Assuming for the moment that the negatives can be projected through A and B, the two projected pictures will coincide in the plane of CD only along a line which will be the contour line on CD. If CD is raised by a contour interval, another contour line may be drawn, and so on. The coincidence of the projected pictures may be established in a variety of ways. If the two pictures are projected with light of different colour and are viewed through appropriate coloured glasses, rendering only each one visible from the corresponding eye, the image will appear in relief on the paper, as in the similar "anaglyph" method of Ducos de Hauron, which the reproductions in the "Illustrated London News" have rendered familiar. The point of a pencil pressing on the paper, and at the same time apparently resting on the surface of the model, will trace a contour line. A modification, probably unpractical, would be to light each negative with white light polarised at 90° from the other, and separate the images with two analysers, as suggested by J. Anderson for showing stereoscopic pictures on a screen. Again either picture might be eclipsed alternately in quick succession, as is done in the "blink" microscope of Pulfrich, producing a steady line between two flickering zones, and this might perhaps be the best method.*

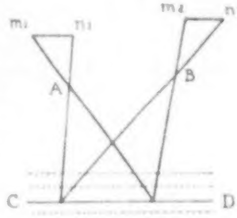

Fig. 29.

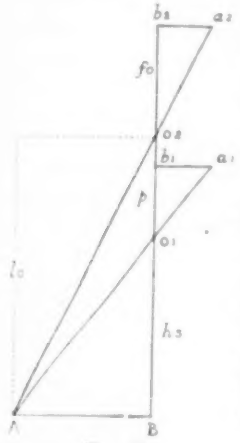

Fig. 30.

Let now (fig. 30) h be the height of one of the air stations O_1 above the plane of AB, s the scale of the plan to be made, and d the contour interval for this plan. Let also a_1b_1 be the negative corrected for tilt in the projection camera, and p its projection distance. The projection AB of a_1b_1 through O_1 cannot be made directly, as was assumed, because AB and a_1b_1 may not be in conjugate foci. To make the projection of $a_2b_2=a_1b_1$ through some other point O_2 in the vertical of O_1 coincide with AB we must have

$$\frac{p}{hs}=\frac{f_0}{l_0},$$

* [The same principle has been used in the "Camera Plastica" recently developed by Nistri in Rome, Gasser in Germany, Nelles in Canada, and others, but so far with indifferent results. H. G. F., Sept. 1926.]

and for AB to be a conjugate focal plane of a_2b_2, f being the focal length of the lens used for the projection,

$$\frac{1}{f_0}+\frac{1}{l_0}=\frac{1}{f},$$

which give

$$f_0=f\left(1+\frac{p}{hs}\right)$$

and

$$l_0=f\left(1+\frac{hs}{p}\right).$$

The points on the contour for AB will alone be correctly projected on the plan. For any other contour hs becomes $s(h-nd)$, where n is the number of contour intervals above the datum AB, so that

$$f_n=f\left(1+\frac{p}{s(h-nd)}\right)$$

and

$$l_n=f\left(1+\frac{s(h-nd)}{p}\right).$$

These expressions may be written

$$l_n=\mathrm{A}+n\mathrm{B},$$

$$f_n=f+\frac{1}{\mathrm{C}+n\mathrm{D}},$$

where $\mathrm{A}=f\left(1+\frac{hs}{p}\right)$, $\mathrm{B}=-\frac{fsd}{p}$, $\mathrm{C}=\frac{hs}{pf}$, and $\mathrm{D}=-\frac{sd}{pf}$ are constants for the pair of plates.

A suitable apparatus for the construction of maps by the interference method would consist of a horizontal board for the plan and two graduated vertical slides with holders for the lenses and negatives, the slides to be adjustable apart to a distance equal to the horizontal length of the base on the scale of the plan. To restrict the projecting rays to an angle within the optical field, the focal length of the lenses used for the projections should not be less than that of the camera lens.

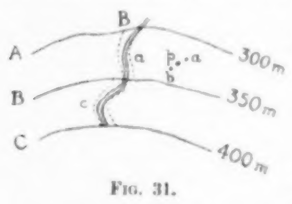

Fig. 31.

The filling in of the details in the zone between two contours may proceed by tracing their outlines in pencil, first with the projection for one of the contours, then with the projection for the other contour, and inking in interpolated lines (fig. 31). As a rule the two pencil lines will be only a fraction of a mm. apart and no appreciable graphical error will result

from the interpolation, but their interval may be made as small as we please by increasing the number of contour lines. Similarly, two close positions a and b being given for a point P, its map position may be interpolated at sight, by dividing the interval in the same proportion as the distances of the point from the two contour lines, without sensibly increasing the ordinary error of plotting.

Stereoscopic Method.—If the two photographs, which may now be positives, have been rectified to a common plane containing the base and any horizontal line perpendicular to the base, they can be placed in a stereoscopic measuring-machine such as that of Fourcade (1901), or the Stereocomparator of Pulfrich (1902), which have been described or referred to in preceding papers, and the position of any point common to the two plates computed, or plotted with a suitable graphical attachment.

Experiments by Prof. Melvill Jones and Major J. C. Griffiths, carried out at Cambridge,* have established that it is possible to fly an aeroplane sufficiently straight and level to reduce to some 40 feet the probable variation in height, from the mean of a flight, of the air stations occupied at the instants of exposure and to 1° from the vertical the probable error of tilt of the plates exposed. The inclination of a long base, to the horizontal, can therefore be made small.

For a base of inclination α, calling now x and y the plate co-ordinates parallel and perpendicular to the base line, and h the height of a point, reckoned from the origin, the ordinary stereoscopic relations become

$$h = -\frac{b}{e}(f \cos \alpha - x_1 \sin \alpha),$$

$$X = \frac{b}{e}(x_1 \cos \alpha + f \sin \alpha),$$

$$Y = \frac{b}{e}y_1,$$

reducing, when α is a small angle, to

$$h = -\frac{b}{e}(f - \alpha x_1),$$

$$X = \frac{b}{e}(x_1 + \alpha f),$$

$$Y = \frac{b}{e}y_1.$$

Other Stereoscopic Methods.—The Stereoautograph of von Orel and Zeiss

* B. Melvill Jones and J. C. Griffiths, "The Mapping of large Areas of Unsurveyed Country," Geographical Journal, June 1923, p. 419.

(1908–10),* the Autocartograph of Hugershoff (1919),† and the Stereoplanigraph of Zeiss (1923)‡ are instruments designed for the direct tracing and contouring of plans from a pair of plates, the position of which in space must previously be known. As these instruments do not depend for their working on a preliminary rectification of the projections, their consideration would be foreign to the subject of this paper, besides which they will be found amply described in the references given. The first is an adaptation of Pulfrich's stereocomparator, and necessitates the use of almost vertical plates. In the other two, a pair of photogoniometers serves as the equivalent of rectified plates, but plates of a tilt as great as 60° must still be used. The great cost and complication of these instruments makes their practical value at present doubtful, and the same may be said of Predhumeau's Stereotopometer (1922),§ which, like von Orel's Stereoautograph, is ill adapted to the use of photographs not taken from the ground. A capital defect of all these instruments is that they cannot utilize horizontal plates, thus throwing away one of the most important advantages which air surveys possess over those from the ground, namely, the possibility of using long bases when the depth of the stereoscopic field need not be great.||

As already mentioned in the introduction, the further application of the stereoscopic method to mapping from air photographs will be considered in later papers. The use of bases much longer than is usual in the practice of stereoscopic surveying from the ground being contemplated, a justification of the procedure will be found in the paper which immediately follows.

Witte Els Bosch,
September 1925.

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* von Orel, E. R., Mitteilungen der k. u. k. militär-geographischen Institutes, vol. xxxi, p. 152 (1911), Vienna, 1911–12. Also C. R. Hinks, "The Stereoautograph," Geograph. Journal, April 1922, p. 273.

† Hugershoff, R. and Cranz, H., *loc. cit.* Also M. N. MacLeod, "The Autocartograph," Geograph. Journal, April 1922, p. 284, and Report of the Air Survey Committee, London, 1923, p. 49.

‡ von Gruber, O., "Der Stereoplanigraph der Firma Carl Zeiss, Jena," Zeisch. f. Instr., vol. xliii, p. 1, 1923. Also Report of the Air Survey Committee, p. 67.

§ Predhumeau, J., "Nouveau Système de Photogrammetrie : Le Stéréotopomètre," Revue d'Optique, vol. i, p. 313, 1922.

|| [Recent modifications of the last three machines have rendered them adaptable for the use of horizontal plates. H. G. F., Sept. 1926.]

ON SOME CONDITIONS FOR THE CORRECT VISION OF STEREOSCOPIC PICTURES.

By H. G. Fourcade.

(With eight Text-figures.)

The stereoscopic perception of relief is not due to the absolute convergence of pairs of visual rays to points of an object, but solely to the difference in convergence of rays to points situated in different distance planes. A pair of stereoscopic views may be moved apart for a considerable range without destroying the combination of corresponding points or altering the apparent relief of the picture. With practice, the convergence may even be made negative. Similarly, a single luminous point in a dark room cannot be located in space from any one position of the eyes, but the addition of a second point will make the relative distance of the two immediately appreciable. These effects may be understood from the circumstance that the two eyes are independent optical instruments, and will receive and convey to the brain the same impression if the images of points continue to occupy the same corresponding points on the retina, whatever, within normal limits, the actual convergence of the optical axes may be. The locus of those points of space which are projected on corresponding retinal points is called the *horopter*, and is dealt with in textbooks of physiological optics.

In normal vision the convergence changes from zero for distant points to about 12° for points at the distance of distinct vision (12 inches or 300 mm.) and a separation of the eyes of $2\frac{1}{2}$ inches = 63 mm. But to every change of convergence is always associated a change in accommodation between limits of infinity and 30 cm. When viewing stereoscopic pictures, accommodation remaining constant, such a wide range of convergence would become unnatural and induce eye strain. To retain natural conditions, the range of convergence must therefore be limited to that for which there would be no sensible change in accommodation when viewing solid objects.

Depth of Focus of the Eye.—If we hold, in a good light, a finely divided scale (such as a slide-rule divided on white celluloid) at a distance of 30 cm. from the eye, another similar scale (the slide of the rule) may be moved about 3·5 cm. further without appreciably decreasing the distinctness of

either scale when both are viewed simultaneously. If we repeat the experiment in sunlight we find that the range of distinct vision has increased to about 6 cm., the explanation being that the pupil having contracted in the intenser light, the diameters of the disks of diffusion forming on the retina the images of points on the scales have decreased in proportion. A more accurate determination may be made with a telescope or equivalent optical apparatus. If we focus the eyepiece on the diaphragm sharply, we find that the telescope can be racked in or out a certain distance for equally good definition of the image of a distant (or optically distant) mark. Using an eyepiece of 29·0 mm. focus and a glass scale divided into tenths of a mm. for its diaphragm, it was found that the distance of the image of a sharp mark could be varied (from the average of a number of measurements) $0{\cdot}595 \pm 0{\cdot}043$ mm. (the p.e. being that of a single measurement) without losing simultaneous good definition of the scale and the mark, when the lighting was such that the pupil was dilated to a diameter of about 2·75 mm., care being taken not to move the eye laterally during a measurement in order to avoid the focussing being influenced by evidence of parallax, which is a more delicate test of focussing than apparent equal sharpness of definition.

The rays between the eye and the eyepiece remaining nearly parallel, we may write with sufficient approximation

$$\frac{1}{f_1}+\frac{1}{f_2}=\frac{1}{f},$$

where f_1 is the focal length of the eye $=15$ mm., and f_2 that of the eyepiece $=29$ mm. For small variations of f_2 we get by differentiation

$$df_1=-\frac{f^2}{(f_2-f)^2}df_2.$$

The numerical values being $\Delta f_1=-0{\cdot}0797$ for $\Delta f_2=\frac{0{\cdot}595}{2}=0{\cdot}298$ mm., Δf_2 is taken at half the mean range of focussing because this range is that of plus and minus distances from the diaphragm.

In an eye of 15 mm. focus we get for points at a distance of 300 mm. (the distance of distinct vision) a conjugate focus $f_1=15{\cdot}7896$ mm. The depth of focus of f_1 being 0·0797, we get further for $f_1=15{\cdot}7896-0{\cdot}0797=15{\cdot}71$ mm., a conjugate focus $f_2=332{\cdot}0$ mm., which agrees tolerably well with the value of 335 mm. obtained from the direct experiment.

Following, to some extent, the treatment of the same point by Caze,* let (fig. 1) O be the aperture of the pupil and R the retina. Two points A and B at distances d and $d+l$ will form when viewed simultaneously

* L. Caze, Stéréoscopie de précision, Paris, 1895, p. 35.

images at C and D, which will be projected on the retina as disks of diffusion of diameter e. When the disks of diffusion are equal,

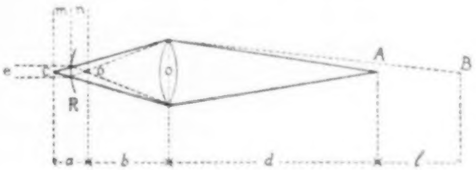

FIG. 1.

$$\frac{e}{o}=\frac{m}{a+b}=\frac{n}{b}=\frac{m+n}{a+2b}=\frac{a}{a+2b},$$

therefore

$$\frac{a}{b}=\frac{2e}{o-e}=k=\frac{2e}{o}, \text{ approx.}$$

Since e is a constant depending on the diameter of the visual elements of the retina (rods or cones), k is also a constant, for a given aperture o of the pupil.

We have also

$$\frac{1}{a+b}+\frac{1}{d}=\frac{1}{f},$$

$$\frac{1}{b}+\frac{1}{d+l}=\frac{1}{f},$$

with

$$\frac{a}{b}=k,$$

from which is derived

$$1+k=\frac{1-\dfrac{f}{d+l}}{1-\dfrac{f}{d}}.$$

When $$d+l=\infty,\ d=\frac{1+k}{k}f.$$

At the distance of distinct vision ($d=300$ mm.) l was found to be 32 mm. giving for $1+k$ the value 1·00507. For $d+l$ infinity and a pupil 2·75 mm. in diameter d becomes 2·97 m., say 3 m. This distance is that of the *punctum remotum* of vision, or *hyperfocal distance*, beyond which no accommodation is required. The hyperfocal distance is usually stated to be about 65 m., which is evidently quite wrong, since such a value would imply that the eye is capable of appreciating differences of 0·3 μ on the retina,

or about one-fifteenth part of the diameter of one of its structural elements.*

We had $\frac{2e}{o} = k$, giving

$$e = \frac{ok}{2} = \frac{2{\cdot}75 \times 0{\cdot}005\!\cdot\!07}{2} = 7\ \mu.$$

The diameter of the cones in the most sensitive area of the retina is about $4{\cdot}5\,\mu$, so that change of accommodation is not sought until the image of a point covers perceptibly more than one of the visual elements.

Helmholtz's experiments indicated that the eye is capable of separating two points when their angular distance apart is more than 1′, which corresponds approximately to the diameter of a visual element. The more recent experiments of Wülfing, Pulfrich, Heine, and others tend to show that the resolving power of the eye may be twice as great, or even more. This is explained by the fact that the eye is never still, and in consequence the images of points continually move over different visual elements. Images nearer together than the diameter of an element will then fall part of the time on two contiguous ones, $1/n$ of the time if the separation is $1/n$ of a diameter (assuming no inert boundary and point images). When n is not more than 2 or 3 the intensity of the second fainter impression may remain sufficient to effect resolution.

The stereoscopic perception of depths is again keener than would correspond to the limit of resolution for single points, because it is derived from the simultaneous perception of the position of groups of points, and the mean error for the mean of each group will be less than the mean error for a single point. The probable errors of stereoscopic bisection in the author's measuring stereoscope, which are given in previous papers, would correspond to a resolving power for each eye of about 15″, and with very well-defined marks still less. Similarly, each eye singly is capable of bisecting a mark in a micrometer microscope or with the telescope of a theodolite with an accuracy 3 or 4 times greater than a resolving power of 30″ for magnification 1.

The hyperfocal distance, the resolving power of the eye, and the stereoscopic perception of depth cannot, therefore, be deduced from one another. Each requires to be determined independently by experiment, with no preconceived idea of the relations between them. The more extreme values obtained for the resolving power by some of the later experimenters are vitiated by the assumption that it is deducible from the measurement of the stereoscopic perception of depth.

* Caze, *loc. cit.*, p. 35, gets 3·30 m. for the hyperfocal distance, a value which agrees with that given above when the aperture of the pupil is made 3 mm.

For eyes 63 mm. apart, the difference of the convergence to points 300 and 332 mm. distant is 0·02 (=tan 1° 7′), which may be taken as the permissible variation in convergence within one field of vision when there must be no change in accommodation. At the same time, to retain entirely natural conditions, the absolute convergence should not be less than zero (parallel rays) nor greater than 0·21 (=tan 11° 52′).

In a stereoscopic measuring-machine, where much convergence would operate detrimentally by reducing the optical field, there is no need to make it greater than is sufficient for the avoidance of negative values. A decentering of each mark by 0·5 mm. for 30 mm. eyepieces, giving a convergence equal to that for a point 1·90 m. distant, will generally be found ample to afford easy vision.

The depth of the stereoscopic field satisfying the convergence condition is given by

$$d = \frac{0{\cdot}02\,Y_2^2}{mB + 0{\cdot}02\,Y_2},$$

where B is the length of the base, m the magnification given by the viewing apparatus ($=F/f$ the ratio of the focal lengths of the camera lens and the viewing lens), and Y_2 the distance of the farther plane of the stereoscopic field.

For, in fig. 2, the permissible relative convergence being $\frac{0{\cdot}02}{m}$, we have

$$\frac{pm}{0{\cdot}02} = \frac{Y_2 - d}{1}$$

$$\frac{p}{d} = \frac{B}{Y_2},$$

from which the value of d given above follows.

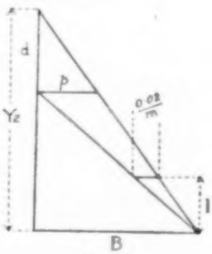

Fig. 2.

The formula may also be written

$$d = \frac{0{\cdot}02\,Y_1^2}{mB - 0{\cdot}02\,Y_1}.$$

where $Y_1 = Y_2 - d$ is the distance of the front plane of the stereoscopic field. We also can deduce, for the length of the base,

$$B = \frac{0{\cdot}02\,Y_2(Y_2-d)}{md} = \frac{0{\cdot}02\,Y_1(Y_1+d)}{md} = \frac{0{\cdot}02\,Y_1Y_2}{md}.$$

For $m=1$, values of d are :

B =	Y = 1.	2.	3.	5.	10.	15 km.
Km.						
0·10	0·17	0·57	1·12	2·50		
0·20	..	0·33	0·69	1·67	5·00	
0·30	..	0·23	0·50	1·25	4·00	7·50
0·50	..	..	0·32	0·83	2·87	5·63
1·00	..	..	0·17	0·45	1·67	3·46
1·73	..	..	0·11			

But it is important to remember that bad lighting, by increasing the diameter of the pupil, would decrease the value of d.

Relief of the Picture.—For magnification 1, the relief is that of a model

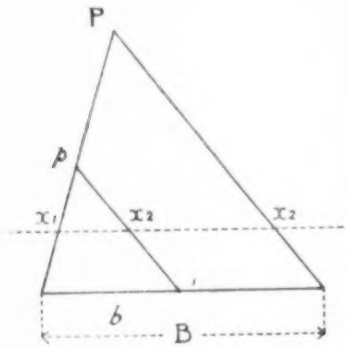

Fig. 3.

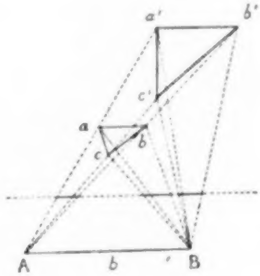

Fig. 4.

on a scale $\frac{b}{B}$ ($b=63$ mm.) when the eyes are placed at the ends of the base on the model. This follows from the similitude of the triangles in fig. 3, where P is any point on the ground, p the corresponding point on the model, and x_1, x_2 the positions of the point on the two plates. The relief being determined by relative, not by absolute, convergence, there are also an infinity of other models which will give the same apparent relief. Thus,

in fig. 4, $a'b'c'$ and abc, which present from A and B the same pairs of pictures at unit distance, will appear identical in shape and size. To compare apparent relief when the convergence is made constant, as in the case of a stereoscopic measuring-machine, it is therefore necessary to refer the relief of a small element of the picture to some arbitrary distance, which may conveniently be that of distinct vision (30 cm.).

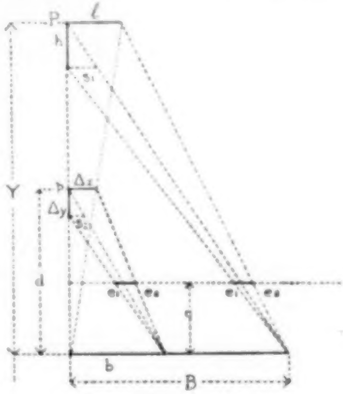

Fig. 5.

In fig. 5, B is the base and P a point on the ground, p the corresponding point in the optical model referred to a distance d from the eyes, the separation of which is b. Let l be a small length on the ground, parallel to the base, h a small distance perpendicular to the base, Δx, Δy the corresponding lengths in the model, and e_1, e_2 the lengths on the plates which h l, and therefore Δy, Δx, subtend from the corresponding ends of b and B. We have

$$\frac{l}{e_2}=\frac{\mathrm{Y}}{q}=\frac{s_1}{e_1},$$

$$\frac{h}{s_1}=\frac{\mathrm{Y}}{\mathrm{B}}.$$

Similarly,

$$\frac{\Delta x}{e_2}=\frac{d}{q}=\frac{s_2}{e_1}, \qquad \frac{\Delta y}{s_2}=\frac{d}{b},$$

whence

$$\Delta y=\frac{h\mathrm{B}d^2}{b\mathrm{Y}^2}, \qquad \Delta x=\frac{ld}{\mathrm{Y}},$$

and

$$\frac{\Delta y}{\Delta x}=\frac{\mathrm{B}d}{b\mathrm{Y}}\cdot\frac{h}{l}.$$

For

$$\frac{h}{l}=1, \quad \frac{\Delta y}{\Delta x}=\frac{\mathrm{B}d}{b\mathrm{Y}}=c,$$

which may be called the coefficient of relief.

When $b=63$ mm. and $d=30$ cm.,

$$c=\frac{300}{63}\cdot\frac{\mathrm{B}}{\mathrm{Y}}=4{\cdot}8\frac{\mathrm{B}}{\mathrm{Y}}.$$

Coefficients of relief for d = 300 mm.

B.	Y = 1.	2.	3.	5.	10.	15 km.
Km.						
0·1	0·47	0·24	0·16			
0·2	0·95	0·47	0·32	0·19		
0·3	..	0·71	0·47	0·28	0·14	
0·5	..	1·19	0·79	0·47	0·24	0·16
1·0	..	..	1·58	0·95	0·47	0·32
1·73	..	..	2·74			

These figures must not be taken to imply that there is any actual compression or elongation in depth of the optical model. The relief with various bases and distances is different only in the same sense that the relief of mountains seen from their vicinity appears greater than when they are observed as part of a distant range, although the actual relief of the ground remains the same.

But to see the optical model correctly it would have to be placed at a distance $\frac{Yb}{B}$ from the eyes. As there is always an equivalent model for any other distance, the distance *d* at which the model is imagined to be will always be some arbitrary distance, but not less than that of distinct vision, nor many times greater. By limiting *d* to that range, the effect will be that with long bases, when *d* would become less than the distance of distinct vision, the relief will appear exaggerated, and with short bases, when the correct position of the model would be many times that of distinct vision but it cannot be imagined so far, objects will appear flattened into a succession of vertical screens. This last effect is well seen in ordinary stereoscopic pictures of scenery, taken with very short bases through improper appreciation of the conditions of stereoscopic vision. The aim apparently is to give to scenery the natural relief with which it is seen in ordinary vision, but this is of little advantage, because perception of relief becomes very feeble beyond 100 m. and ceases altogether beyond 450 m. It will be found of far greater interest and instruction, whether with scenery or architectural subjects, to produce smaller-scale models representing the relief correctly at a distance which it would be natural to view such models from if they were solid.*

Effect of Magnification.—The relative relief is independent of the magnification given by the viewing apparatus, heights, or widths, and the

* Views of European cathedrals and Swiss mountains, taken by the author in 1903, make fascinating models, very unlike those resulting from short bases.

stereoscopic differences determining depths being all increased simultaneously in proportion to the power used. Thus a body which appears spherical under magnification 1 will remain apparently spherical with any other magnification.

This is in contradiction of the view, advanced in the article "Stereoscopy" in the Encycl. Brit. (11th ed., vol. 25, p. 897), for which support is wrongly claimed from Helmholtz, that the action of base magnification is radically different from that of telescope magnification: "In the first case the three-dimensional image is a model proportionately diminished in all its dimensions and brought nearer to the observer, in the other the objects appear pushed together to the front like the wings of a theatre," which, being read together with the further statement that in the second case, "as the distances are lessened the areal dimensions remain unchanged," is taken to mean that magnification will cause a compression of the optical model, which is never the case.

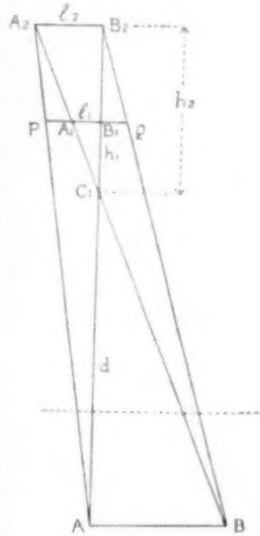

Fig. 6.

In fig. 6 let h_1 be the depth of an object in the optical model seen with magnification 1, and $A_1B_1=l_1$ the portion of its width at B_1 intercepted by the rays AC_1 and BC_1. When the magnification is m and the point C_1 is kept fixed on plates A and B, from B, A_1B_1 will become $A_1Q=ml_1$, and, from A, A_1B_1 will become $PB_1=ml_1$. The intersection of the rays BQ and AC_1B_1 will be at B_2, and that of AP and BC_1A_1 at A_2, and $A_2B_2=l_2$ parallel to A_1B_1 will be the magnified image of A_1B_1. C_1 remaining the same with both magnifications, we have

$$\frac{h_1}{h_2}=\frac{l_1}{l_2},$$

$$\frac{ml_1}{l_2}=\frac{d+h_1}{d+h_2},$$

whence

$$\frac{h_2}{h_1}=\frac{md}{d-h_1(m-1)},$$

reducing, when h_1 is small, to

$$\frac{h_2}{h_1}=m.$$

When $\frac{b}{B}=\frac{1}{n}$ and $m=n$, the object having been first transformed into a model on a scale $1/n$, then enlarged n times, will appear in natural size and shape at C_1. This gives the so-called "Helmholtz rule," which is erroneously disputed by Pulfrich in the Encycl. Brit. article referred to. A glance at the same pair of views alternately in an ordinary stereoscope, with magnification 1·1, and in the measuring stereoscope of the author, giving magnification 7 when eyepieces of 20 mm. are used, is sufficient to form an experimentum crucis, which confirms the soundness of Helmholtz' views and negatives their correction by Pulfrich. There is no perceptible difference in the apparent shape of any parts of the two models. The only difference is one of size.

Far from there being any compression, it may be computed from the relations connecting l_1, l_2, h_1, h_2, m, and d that there will actually be a slight elongation in depth of an image when it is magnified, but too small to be noticeable. For m greater than unity the equation of a sphere transforms into that of a prolate ellipsoid of revolution, differing little from a sphere, with its major axis perpendicular to the base and its pole at a distance d from the base. The equation of the generating curve is, taking C_1 for the origin,

$$X^2+Y^2\left(1-\frac{2r(m-1)}{d}\right)-2rmY=0,$$

and the length of the semi-major axis—that is, the distance of the centre of the ellipse from C_1—will be

$$a=\frac{rm}{1-\frac{2r(m-1)}{d}},$$

where r is the radius of the sphere under magnification 1.

Example.—The diameter of a sphere seen under magnification 1 is $d/10$. With magnification 7

$$a=\frac{7r}{1-\frac{2\times 6}{20}}=7{\cdot}4r.$$

For extreme cases which cannot occur in practice, the image of a sphere would become magnified into a paraboloid when $\frac{r(m-1)}{d}=2$, or a hyperboloid when $\frac{2r(m=1)}{d}>1$. It always remains an ellipsoid when $\frac{2r(m-1)}{d}<1$. The x-diameter of the sphere transforms not into the diameter of the

ellipsoid, but into the chord at distance h_2. The actual elongation must therefore be derived from the formula first given, and not from the ratio of the diameters of the sphere and the ellipsoid. For the example given it will be

$$\frac{h^2-mr}{mr}=\frac{d}{d-r(m-1)}-1=1\cdot03,$$

or 3 per cent.

Choice of Length of Base.—If it is intended to include in one view the whole of the model determined by the pair of plates, as when the photographs are those of architectural subjects or are designed to give natural representations of topographical forms or picturesque scenery, the length of the base should not exceed the value derived from the preceding formula. But when measurement of the relief is the main object, the depth of the stereoscopic field need at most only be equal to that of the portion of the model seen at one time in the viewing apparatus. And when attention is confined to the making of bisections with a mark or the tracing with that mark of a feature or contour line, the field of distinct vision for which common accommodation is necessary becomes restricted to a vertical angle of about 2° and a horizontal angle of about 4°, corresponding to the size of the "yellow spot" in the centre of the retina. Even if in this limited field the depth of the features sometimes exceeds that of the stereoscopic field, as may happen when viewing precipices from the air, the occasional strain on the eyes will be no greater than when trying to observe simultaneously a pair of rifle-sights and a target.

Bases in Plains.—The stereoscopic method cannot be applied from ground stations to quite level country, because the distances even in the restricted field of vision will then generally differ by more than the depth of the stereoscopic field, unless the base is made so small as to be useless for measuring purposes.

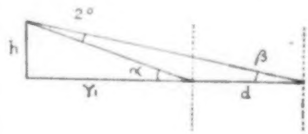

FIG. 7.

In fig. 7, where h is the height of the base above the general level of the country, and Y_1 the distance of the front plane of the stereoscopic field, the length d seen within a vertical field of 2° must not be greater than the depth of the stereoscopic field. When h is small, with sufficient accuracy,

$$\frac{h}{Y_1}=\tan\alpha=\sin\alpha \quad \text{and } \cos\beta=1,$$

so that

$$\frac{d}{\sin 2^\circ}=\frac{Y_2}{\cos\beta\sin\alpha}=\frac{Y_2Y_1}{h},$$

or, with magnification m,

$$d=\frac{0{\cdot}035\text{Y}_2\text{Y}_1}{mh}.$$

We had previously for the depth of the stereoscopic field,

$$d=\frac{0{\cdot}02\text{Y}_2\text{Y}_1}{\text{B}m},$$

whence the condition, for level country,

$$\frac{0{\cdot}02\text{Y}_2\text{Y}_1}{\text{B}m}>\frac{0{\cdot}035\text{Y}_2\text{Y}_1}{mh},$$

or

$$\text{B}<0{\cdot}6h.$$

Bases in Hilly Ground.—The method is much more applicable to hilly or mountainous country.

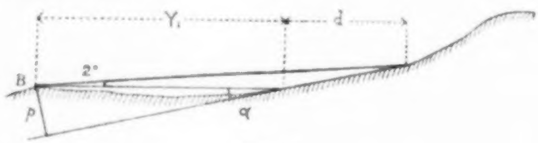

Fig. 8.

In fig. 8, B is the location of the base and d the horizontal depth of a slope seen within a vertical field of 2°, the inclination of the slope towards the base being α. Then

$$\frac{p}{\text{Y}_1}=\sin\alpha,$$

$$\frac{\sin 2^\circ \cos\alpha}{d}=\frac{\sin\alpha\cos 2^\circ}{\text{Y}_2},$$

whence, with magnification m,

$$d=\frac{\text{Y}_2\tan 2^\circ}{m\tan\alpha}=\frac{0{\cdot}035\text{Y}_2}{m\tan\alpha}.$$

We have again for the depth of the stereoscopic field,

$$d=\frac{0{\cdot}02\text{Y}_2\text{Y}_1}{\text{B}m},$$

giving now the condition

$$\text{B}<0{\cdot}57\text{Y}_1\tan\alpha.$$

Values of $0{\cdot}57\ \text{Y}_1\tan\alpha$ for slopes at an inclination α towards the base are as follows :—

Y_1.	$a=10°$.	20°.	30°.	40°.
Km.				
1	0·10	0·21	0·33	0·48
2	0·20	0·41	0·66	0·96
3	0·30	0·62	0·99	1·44
5	0·50	1·03	1·44	
10	1·00	2·07		
15	1·50			

The use of sufficiently long bases is therefore generally practicable.

Application to Air Surveys.—But it is from the air that the power of the stereoscopic method becomes the greatest. It has wrongly been assumed from the analogy of ground surveys that the method always demands the use of comparatively short bases. We have seen that the longer the base, the less the depth of the stereoscopic field. On the ground this depth represents differences of horizontal distances. But from the air it represents only differences in height. Hence air bases, when horizontal plates are exposed, can easily be made several times the length of those on the surface of the ground, without detriment to stereoscopic combination, which it should be remembered is independent of absolute convergence. The relief will appear exaggerated, but the viewing of an optical model in which the vertical scale is larger than the horizontal scale will present no greater difficulty than the viewing of a model in which both scales are kept equal.

Witte Els Bosch,
September 1925.

A NEW METHOD OF AERIAL SURVEYING.

By H. G. Fourcade.

(With eighteen Text-figures.)

The method is based upon the following theorem :—

The correspondence between the pencils of rays joining two centres to any number of points in space is uniquely determined if to five rays in the one there are given the corresponding five rays in the other, provided no three pairs of the rays lie in a plane.

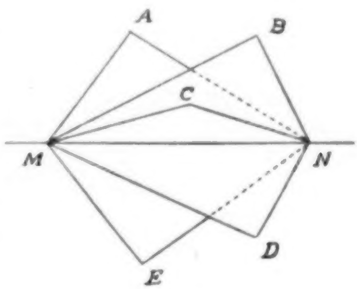

Fig. 1.

To prove this, let $ABCDE$ (fig. 1) be five points in space joined by pencils of rays from M and N. Displace along MN the pencil from M, parallel to itself, until M coincides with N, and describe a sphere of arbitrary radius, from centre N, on which the directions of the rays from N will be represented by points and the five basal planes by great circles intersecting along MN.

If a and a' (fig. 2), the directions of A, are made coplanar with MN the condition that b and b', the directions of B, are also coplanar with MN will give an equation denoting that the polar angle between a' and b' is equal to the polar angle between a and b. The other three pairs of points will also give with the first pair three similar equations which, together with the first, determine the unknowns $x_1x_2y_1y_2$ and the two figures $abcde$ and $a'b'c'd'e'$, since either is determined when two of its points are determined.

For one or two of the equations one or two conditions between the points in space may be substituted. For instance, if four points of the figure in space lie in a plane, the four pairs of rays to them become sufficient to determine the correspondence of the two pencils provided no three of the points lie in a line, this particular case being a proposition already established in the projective geometry of quadric surfaces. When two

point conditions are given—that is, two angles of the triangle formed by three points—the case reduces to the ordinary problem of resection in space, and three pairs of rays determine correspondence.

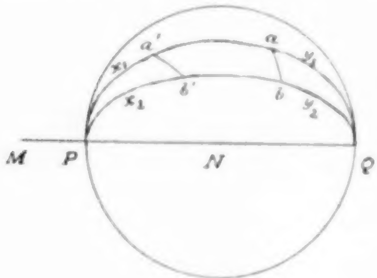

Fig. 2.

Five points common to two photographs, of which the centres of projection are known, determine two pencils of five rays of which the correspondence, and therefore that of the photographs, is determined.

Theory of the Stereogoniometer.—The stereogoniometer is an instrument for setting, without computations, two photographic plates in correspondence. When they have been so set, the co-ordinates of any point common to the two plates may be readily computed. Or, with the addition of a mapping attachment, orthogonal projections and contour lines may be drawn directly from a pair of negatives. To determine the scale and draw a map which is a projection on a horizontal plane, it is necessary to know the positions of three points on the ground which are also represented on the pair of photographs, but it is possible to continue linking other photographs to the first pair without any further reference to the ground. As with ground traverses it is, however, desirable to close an aerial traverse on to fixed points. Compensation may be provided throughout for the effects of curvature and refraction.

Fig. 3 is a diagram of the instrument. Two photogoniometers are mounted on a horizontal "polar" axis which corresponds to the *MN* of fig. 1, each being capable of independent rotation round that axis. The photogoniometers can also rotate round "declination" axes, through *P* and *Q*, at right angles to the polar axis, and the plates can turn in their own planes about "normal" axes *PR* and *QS*, which are the plate normals, at right angles to the declination axes. By construction, the three axes pass through the front nodal point of the lens, but this condition need only be approximate. By means of these movements the plates may be set at any inclination or orientation to each other, and the pair may be rotated together round the common polar axis without disturbing their correspondence.

In front of the polar axis, and parallel to it, is a slide carrying two sets of sextant mirrors *cd* and *c'd'*, the object of which is to reflect the rays through the photogoniometer lenses into a fixed binocular double telescope fitted with two sighting marks, *tt'*. By displacing the mirrors on the slide

the picture is traversed horizontally, and by rotating the pair of photogoniometers together round the polar axis it is traversed vertically so that any portion of the image may be brought into the field of the telescope, where it appears in stereoscopic relief. Graduated circles, or portions of circles, on the instrument record the various rotations.

The deflection to the telescopes of any horizontal ray through the lenses is effected in the following manner. Mirror *c* is fixed to the carrier at a constant angle, while mirror *d* and the arm *dh* rotate together round a vertical axis at *d*. Another arm, *efi*, is pivoted at *f* on the carrier. The point *e* is constrained to remain on the line *dh* and the line *fi* to pass through the fixed point *g*. If *gf* is made equal to *dP* and *gP* to *fd*, *gf* and *Pd* will

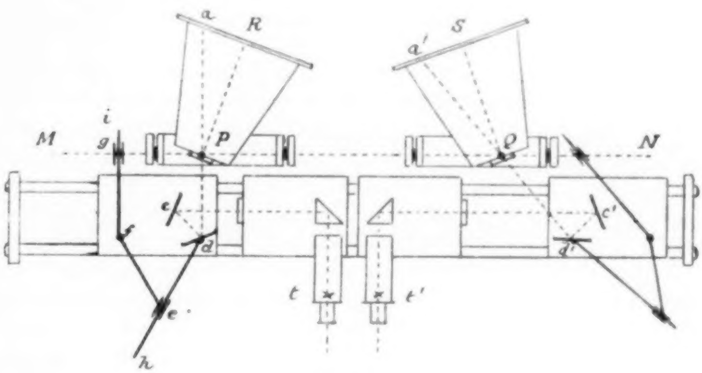

FIG. 3.

remain parallel for all positions of the carrier on its slide, and if, further, *fd* is made equal to *fe*, *fde* being an isosceles triangle the rotation of *dh* and its attached mirror *d* will always be half that of *fi* or *Pd*, so that rays of any incidence through *P* may be reflected to any constant direction *dc* and thence to that of the optical axis of the telescope.

The angle which a ray makes with the polar axis is then given by double the amount of rotation of the moving mirror from a zero on the carrier, which is the reading for a ray perpendicular to the polar axis, and since the rays between the photogoniometer lenses and the telescope objectives are parallel rays and the pair of mirrors *c* and *d* reflect the rays at a constant angle for any given position of *d* relatively to the carrier, the error of the measurement will be independent of any inaccuracy in the mechanical movement or in the slides.

If the longitudinal slide is made sufficiently straight, which seems feasible, the fixed mirror may be dispensed with and the rays reflected directly into

the telescope, the right-angled prism in the latter being replaced by a double reflection prism to preserve the erection of the image. And if the mechanical movement rotating the mirror is accurate the longitudinal travel of its carrier will be proportional to the cotangent of the angle the rays make with the polar axis.

Fig. 4 shows an experimental model of the apparatus, the parts for which were constructed towards the end of last year. The lenses used in the photogoniometers are two Zeiss "Amatar" lenses of $f/6{\cdot}8$ aperture, nominal focal length 150 mm. and actual focal length 141·0 mm. at full aperture. The telescope lenses are of 1 inch diameter and 8 inches focal

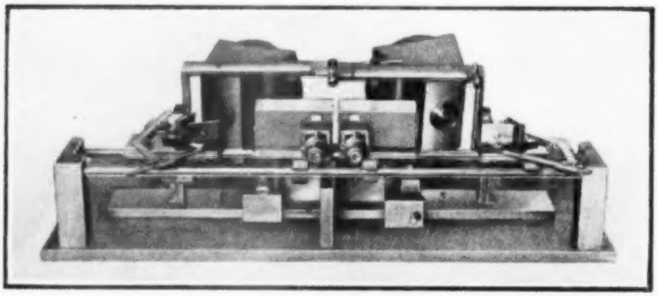

Fig. 4.

length, giving with 1-inch eye-pieces magnification 8. The mapping attachment is wanting.

The angle with the base at which the views are taken has no effect on the apparent size or relief of the image, which remains exactly the same as if the plates had been exposed in one plane, using a lens capable of taking the angle. The appearance of the picture is that of a relief map hung vertically on a wall and examined in detail from the distance of distinct vision. The rotation of the mirrors causes no corresponding rotation of the image.

When the ratio of the length of the aerial base to its height above the ground exceeds the ratio of the separation of the eyes to the distance of distinct vision (that is, is greater than one to four or five), the relief will become exaggerated, becoming similar to that of a relief map in which the vertical scale is larger than the horizontal scale. It has been shown by the author in a previous paper * that when the base is approximately parallel with the ground, very long bases may be used over ordinary country without

* "On Some Conditions for the Correct Vision of Stereoscopic Pictures," Royal Society of South Africa, Oct. 21, 1925.

exceeding, in any portion of the image seen at one time, the depth of the stereoscopic field. Bases of three-fourths the height, or even longer, will usually be found quite practicable. In mountainous country the length of the base may have to be reduced, or flying carried at a higher altitude. But, on the other hand, it is here that the ground method of stereoscopic surveying, published by the author in 1901,* and, independently, by C. Pulfrich in 1902,† finds its best application. The two methods are complementary.

In the absence of a knowledge of the vertical, horizontal plates are badly conditioned for setting into correspondence. Inclined plates are therefore to be preferred. The accuracy of the setting of these increases with their inclination and with the ratio of the base to its height above the ground. The inclination is limited by the angle of the lens, which, again, is limited by its aperture. A suitable lens is one of $f/6{\cdot}8$ aperture covering a field of 70° at full aperture. This corresponds to a diameter of 52° 40′ on a square plate, which is further reduced to 45° to allow for unavoidable swing of the camera.

Camera.—A pair of cameras inclined to each other at an angle of 45° is required for the securing of forward and back pictures from each station (fig. 13), but a battery of four cameras, composed of two pairs at 45° taking separately the ground to the right and to the left of the base-line, may be preferred in order to double, or more, the area covered by a flight without increasing the number of positions to be determined or of settings of the apparatus. The design of the cameras is straightforward and need not be considered at this stage.

Definitions.—Before proceeding further, it becomes necessary to define a few terms that will be needed. Following the method of crystallographers for the study of the relations between the faces of a crystal,‡ the direction of the plane of a plate in space may be referred to the sphere of arbitrary radius already made use of and similar to the celestial sphere of astronomy. And adopting the practice of writers on perspective, the *principal point* of a plate will be defined as the foot of the perpendicular from the back nodal point of the lens to the plane of the plate. The perpendicular itself will be called the *plate normal.*

In fig. 5, Z is the zenith and NS the meridian. AB are the points at which two planes parallel to those of the plates are tangent to the sphere of reference. Since the centre of the sphere corresponds to the back nodal

* "On a Stereoscopic Method of Photographic Surveying," South African Philosophical Society, Oct. 2, 1901.

† "Ueber neuere Anwendungen der Stereoskopie und über einen hier für bestimmten Stereo-Komparator," Zeitschrift für Instrumentenkunden, March, May, and August 1902.

‡ *e.g.* Mallard, Traité de Cristallographie (1879), vol. i, p. 62.

point of the lens, the spherical co-ordinates of A and B are those of the two plate principal points, and the pictures on plates A and B, viewed from above the convex sphere, will appear as on the ground-glass of a camera. Rotations on the sphere will be considered positive if to the left hand, and negative if to the right hand. This is equivalent to positive right-hand rotations of a negative plate viewed from the film side, and to negative right-hand rotations of a positive print. The *inclination* of Plate A is then given by the zenith distance ZA of its normal, its *azimuth* by the azimuth NZA of the normal, reckoned N. by W. on the sphere, and its *deviation* by the angle ZAx which a line through the principal point and parallel to the plate x-axis makes with the great circle containing Z and A, the deviations being reckoned N. by W.

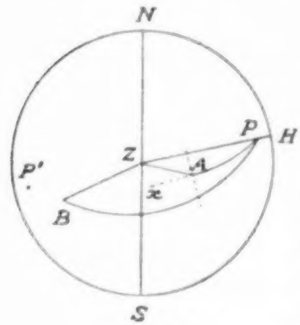

FIG. 5.

The points P and P' at which the line joining the two air stations, that is, the front nodal points of the two lenses, intersects the sphere of reference (PQ of fig. 2) are called the *poles* of the pair. PA and PB are now the *polar distances* of the two plates, always reckoning from the right-hand pole. The angle at P which PB makes with PA, reckoning counterclockwise, is the *polar bearing* of B. The angle which a parallel, through A, to the plate x-axis makes with the great circle through A and P is the *position angle* of Plate A, reckoned counterclockwise from the direction of the great circle PA. Lastly, the trace of the median plane perpendicular to the polar axis is called the *equator* of the plate.

The following is the correspondence between the two systems of spherical co-ordinates and the symbols that will be used in referring to them :—

Azimuth, a	Polar bearing, λ
Inclination, i	Polar distance, Δ
Deviation, ψ	Position angle, ω.

$PH=\frac{\pi}{2}-ZP$ is the inclination of the base, and NZP its azimuth.

When two plates exposed together from an air station are constrained to have their y-axes parallel and their x-axes at a constant angle, the two plates are said to be *linked* at an angle which is the angle between their normals.

The circles of the instrument are, besides the *direction circle*, on which the polar bearings are read, the two *declination circles*, measuring the

rotations of the two mirrors and the two *position circles* measuring rotations of the plates in their own planes. A single linear scale, measuring the displacements of the two mirror carriers, may be substituted for the two declination circles.

Setting of the Plates.—The simplest case is that in which the base ratio is so chosen that the optical axes converge approximately to the same point of the ground. This point will then be at the centres of both plates, and having been set in correspondence will remain in correspondence for any rotation of either position circle. For any small rotation of either plate round its declination axis every point in the equator of the plate will retain its polar bearing unaltered, while points at a distance from the equator will travel in small circles parallel to the great circle passing through both plate centres, and every point on the diameter through the plate centres will remain in correspondence. These properties allow of each adjustment being made successively without disturbing materially the preceding one, provided the points of reference are suitably selected. It is more convenient and accurate, although not necessary, to make use for the settings of a greater number of points than five. The procedure is as follows:—

(*a*) Set (fig. 6) the points A and B, near the centres of both plates, in correspondence by means of the difference screw. (*b*) Make points GH in the diameter passing through both centres agree with their other images G' and H' by rotating one of the position circles. (*c*) Make a point C' near the equator and a corner of one plate agree with its image C on the other plate by rotating the latter round its declination axis. (*d*) Deal similarly with D and D' by rotating the other declination axis. There will now remain equal terminal discrepancies between E and E' and F and F'. To remove these (*e*) rotate both position circles by an amount given by the terminal discrepancy multiplied by a factor determined on p. 106. (*f*) Restore correspondence between C and C' and D and D' by repeating (*c*) and (*d*). If there is any terminal discrepancy left, repeat (*e*) and (*f*) until it vanishes.

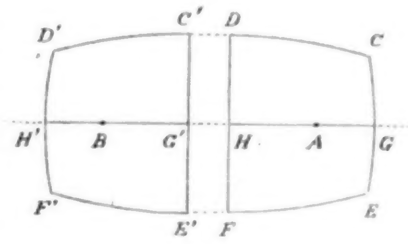

Fig. 6.

When, as generally must be the case, the optical axes do not point to the same spot on the ground, successive approximations must be resorted to, starting from a point midway between the two plate centres. But the approximations are rapidly convergent, so that going over

the settings a second time will usually be sufficient to establish correspondence over the whole of the pair of plates.

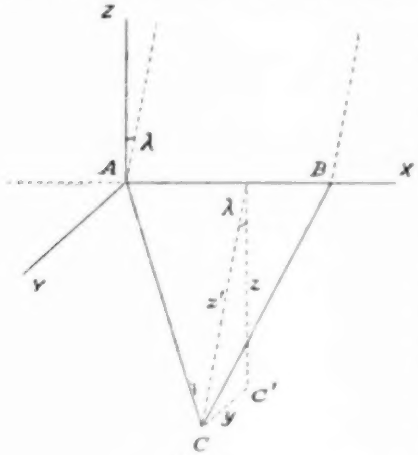

Fig. 7.

Computation of Co-ordinates of Points.—The rectangular co-ordinates of points may be computed, taking A (fig. 7) for origin, the base AB for x-axis, and the perpendicular to the x-axis in the plane containing the pole P as the z-axis.

When the pair of plates have been set in correspondence the polar bearing λ of any point C is the same on both plates. The stereogoniometer gives its reading and also the angles A and B which AC and BC make with the base-line.

The co-ordinates of C are then—

$$x = M \cot A,$$
$$y = M \sin \lambda,$$
$$z = -M \cos \lambda,$$

where
$$M = \frac{b \sin A \sin B}{\sin (A+B)}.$$

Corresponding formulae in terms of linear lengths l_a l_b which are the displacements of the mirror carriers on the slide of the instrument are

$$x = \frac{M}{p} l_a,$$
$$y = M \sin \lambda,$$
$$z = -M \cos \lambda,$$

where $M = \frac{b}{e} p$, e is the stereoscopic difference $l_b - l_a$, and p a constant equal to the distance fg of fig. 3.

If three known points abc are shown on the pair of photographs, their co-ordinates may be computed from an assumed base. Then

$$(x_a - x_b)^2 + (y_a - y_b)^2 + (z_a - z_b)^2 = l^2$$

will give ab on the assumed base, and if the true distance is L, the length of the base will be its assumed length multiplied by L/l. The accuracy

of the result may be tested with *ac* and *bc* and a length adopted for the base derived from the weighted mean of the three ratios obtained.

Let θ be the rotation round the x-axis which will make the plane XZ vertical and $i=PZ$ (fig. 8), the further rotation round the new y-axis which will make the base horizontal. C in the reference triangle ABC being taken as the origin of both sets of co-ordinates, ZA and ZB are the zenith distances at C of A and B corrected for curvature and refraction, *i.e.* the actual angles which the chords CA and CB make with the vertical at C. These data are provided by the ground survey, as also the angles ZBA and ZAB. P is the pole of the pair of plates, BPA the polar angle between A and B and PA, PB the polar distances of A and B on the right-hand plate. We have then

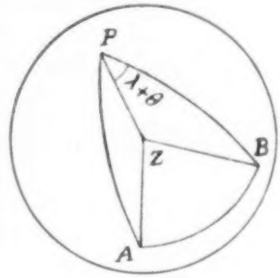

Fig. 8.

$$\sin PBA = \sin PA \sin APB \operatorname{cosec} AB,$$
$$PBZ = PBA - ZBA,$$
$$\cos i = \cos BZ \cos BP + \sin BZ \sin BP \cos PBZ,$$
$$\sin(\lambda+\theta) = \sin ZB \sin PBZ \operatorname{cosec} PZ,$$

where λ is the polar bearing of B. θ and i are now determined.

It may be noted that θ and i are equivalent to two of Euler's co-ordinate angles taken in a different order. It is unnecessary for the present purpose to compute the third, giving the rotation round the axis OZ required to complete the transformation of co-ordinates, because the correction for curvature may be eliminated, as will be shown further, by taking a new origin for each sheet, this allowing the axes of successive systems to be kept horizontal and vertical. The sheets can then be assembled on a map by superposition of the overlaps without having to compute the azimuths of the horizontal axes. These could, however, be readily obtained by computing the angle of direction of ZA or ZB on the horizontal and vertical system of air co-ordinates and comparing with their azimuths supplied by the ground survey.

We may apply θ directly to the polar bearing λ measured in the stereo-goniometer and be left to deal only with the effect of the rotation i. For a positive rotation i ($=\phi$ in fig. 9) we have

$$x' = x \cos i - z \sin i,$$
$$y' = y,$$
$$z' = z \cos i + x \sin i.$$

The co-ordinates corrected to the vertical then become

$$X = M\ (\cot \Delta \cos i + \cos (\lambda+\theta) \sin i),$$
$$Y = M \sin (\lambda+\theta),$$
$$Z = M(\cot \Delta \sin i - \cos (\lambda+\theta) \cos i).$$

i and θ are also the settings, which will make the mapping attachment, to be described later, draw orthogonal projections of the ground, on a horizontal plane, to any scale required, determined by a third setting.

For the carrying of aerial traverses, and for direct photographic rectification when the ground is nearly level, it is required to know the inclination, azimuth, and deviation of a plate. The problem is analogous to the transformation in spherical astronomy of *R.A.* and *N.P.D.* into azimuth and zenith distance. Two other problems will also be considered.

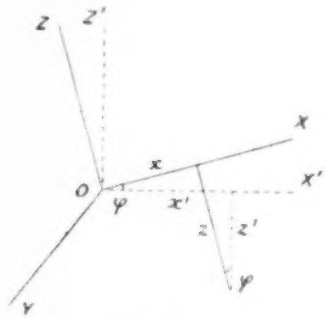

FIG. 9.

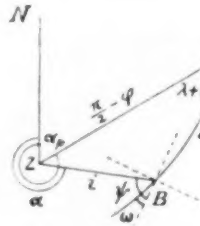

FIG. 10.

First Problem.—In fig. 10, Z is the zenith, P the pole, B the centre of a plate, and N the north meridian. We are given Δ, λ, ω from readings on the stereogoniometer and have computed ϕ, θ, and a_p. The required values of i, a, and ψ are found from the equations

$$\cos i = \cos \Delta \sin \phi + \sin \Delta \cos \phi \cos (\lambda+\theta),$$
$$\sin (a_p - a) = \sin \Delta \sin (\lambda+\theta) \operatorname{cosec} i,$$
$$\sin (\psi - \omega) = \cos \phi \sin (\lambda+\theta) \operatorname{cosec} i.$$

Second Problem.—Equations connecting a pair of linked plates (fig. 11). Given i_1, ψ_1, a_1 and the angle V between the two plate normals, find i_2, ψ_2, and a_2. We have

$$\cos i_2 = \cos i_1 \cos V - \sin i_1 \sin V \cos \psi_1,$$
$$\sin (a_2 - a_1) = \sin V \sin \psi_1 \operatorname{cosec} i_2,$$
$$\sin \psi_2 = \sin i_1 \sin \psi_1 \operatorname{cosec} i_2.$$

Third Problem.—Two plates being in correspondence and i_2, ψ_2, and a_2

given for the one, find i_3, ψ_3, and a_3 for the other, and ϕ, θ, and a_p for the pair. The plates being in correspondence, we know also λ, Δ_2, Δ_3, ω_2, and ω_3 (fig. 12, in which ω_2 is the smaller of the marked angles at A_2). The required equations will then be

$$\begin{aligned}
\sin\phi &= \cos i_2 \cos\Delta_2 - \sin i_2 \sin\Delta_2 \cos(\psi_2-\omega_2),\\
\sin\theta &= \sin i_2 \sin(\psi_2-\omega_2)\sec\phi,\\
\cos i_3 &= \sin\phi\cos\Delta_3 + \cos\phi\sin\Delta_3\cos(\lambda+\theta),\\
\sin(a_p-a_2) &= \sin\Delta_2 \sin i_2 \operatorname{cosec}\theta,\\
\sin(a_p-a_3) &= \sin\Delta_3 \sin i_3 \operatorname{cosec}(\lambda+\theta),\\
\sin(\psi_3-\omega_3) &= \cos\phi\sin(\lambda+\theta)\operatorname{cosec} i_3.
\end{aligned}$$

We have now determined in succession the elements of four plates and two bases, and can continue, by means of the second and third problems,

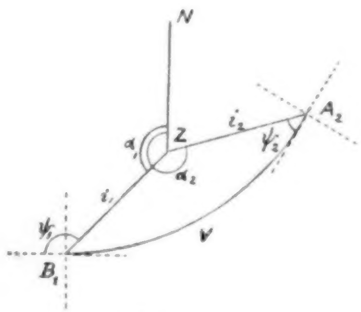

FIG. 11.

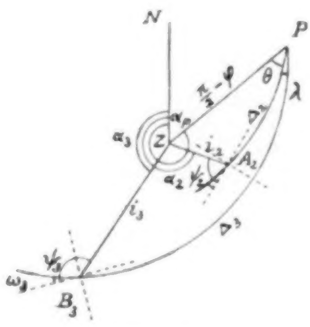

FIG. 12.

adding pairs of plates to an aerial traverse, without reference to the ground, as far as the accumulation of errors in correspondence will allow. The length of each base is obtained by computing from both sides the co-ordinates of two points in the overlap between a pair of bases and comparing the distances on each system.

Curvature and Refraction.—The series of plates being nearly in a straight line, the curvature of the earth may be compensated for by adding to each angle V a correction which is half the angle subtended by the two adjacent bases at the centre of the earth. If the line of the bases is too broken for this method, it is easy to compute the correction more accurately. It has been pointed out by the author in a previous paper * that refraction is best ignored, because the error made in determining the air positions without

* "The Optical Transformation of Projections and its Application to Mapping from Air Photographs," Royal Society of South Africa, Oct. 21, 1925.

reference to refraction is to a large extent reciprocally compensated by the error made in determining back ground-points from apparent air positions, and any residual error left is not cumulative.

Use of Vertical.—If it were possible to indicate the vertical point Z on the plates, the values of i, ψ, ϕ, and θ could be read directly on the stereogoniometer and no computations would be needed for setting the mapping attachment nor for carrying an aerial traverse, since the scale could be determined graphically for each pair of plates by comparing a length with the same length derived from the preceding pair, and the scale setting altered in proportion. Also, in flat country, photographic rectification could proceed at once without reference to ground-points except to supply the scale.

A mirror revolved horizontally by a gyroscope might be made to reflect on to a photographic plate, through a second lens, the line of collimation of a telescope attached to the camera. Half the angular deviation of the image from a fixed mark on the plate would give the distance and direction of the departure from the vertical, subject to the correction for latitude which applies to Admiral Fleuriais' gyroscopic horizon. Whether the accuracy attainable with such a device would be sufficient for the purposes of aerial survey can only be ascertained by experiment.

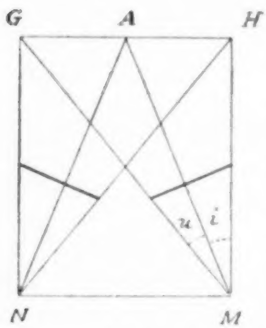

FIG. 13.

Selection of Reference Points.—In order to get numerical relative values of the influence of errors in correspondence on the various settings we must choose definite reference points for establishing the correspondence.

Let (fig. 13) MN be the two air stations, A the point on the ground towards which the optical axes MA, NA converge, and HG two points of the ground in the equators of plates M and N. GH is parallel to MN and passes through A.

The angle NAM being 45° and $AMH = i = 22° \ 30'$, we have

$$\tan (i+u) = 2 \tan i,$$

whence $u = 17° \ 8' \ 20''$ and $(i+u) = 39° \ 38' \ 20''$.

It is convenient to take for the other reference points two points DF on the equator of plate A (fig. 14) at a distance i from AB and their corresponding points $D'F'$ on plate B, together with two points $C'E'$, on the equator of plate B, at the same distance i from AB, and their corresponding points CE on plate A. The points so chosen are near the corners of the used portions of the plates or along diameters of the plates containing AB.

The plates may be set at once accurately in position angle relatively to each other, but the initial setting of either is only a trial one, of which we may compute the error in terms of the terminal discrepancy in correspondence between E' and E and F' and F.

Effect of Change in Position Angle on Polar Bearings of Reference Points.—We shall begin by considering the effect of equal movements $\Delta\omega$ given to the position angles of plates A and B on the polar bearings of the reference point C and its corresponding point C'.

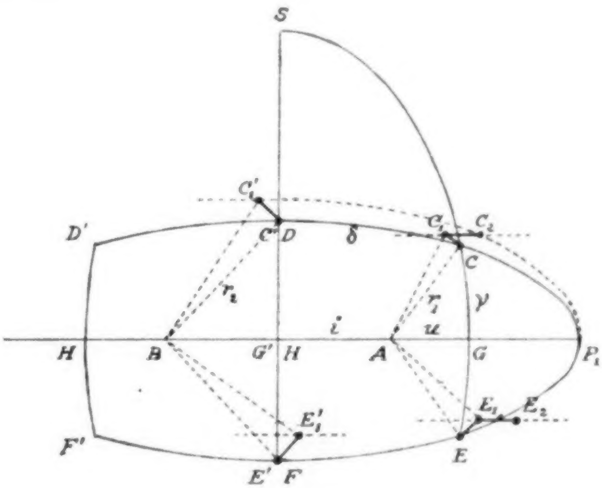

FIG. 14.

From triangle SDC, right-angled at D, in which $SD=\frac{\pi}{2}-i$ and $CSD=i+u$, and from the relation between i and u, we get

$$\begin{aligned}\tan\delta&=\cos i\tan(i+u)\\&=2\sin i.\end{aligned}$$

Similarly, from triangle P_1GC_1, right-angled at G, in which

$$P_1G=\frac{\pi}{2}-(i+u) \text{ and } CP_1G=i, \text{ we get}$$

$$\begin{aligned}\tan\gamma&=\cos(i+u)\tan i\\&=\tfrac{1}{2}\sin(i+u),\end{aligned}$$

whence

$$\begin{aligned}\cos r_1&=\cos u\cos\gamma,\\ \cos r_2&=\cos^2 i.\end{aligned}$$

From the triangles ACP_1 and BDP_1 we get, further,

$$\sin DCA = \sin i \cos i \operatorname{cosec} r_1,$$
$$\sin D'DB = \sin i \cos i \operatorname{cosec} r_2.$$

If small rotations $\Delta\omega$ are given to r_1 and r_2,

$$CC_1 = \Delta\omega \sin r_1,$$
$$C'C'_1 = \Delta\omega \sin r_2,$$

and the increments in the polar bearings of C and C' will be, the letters in parentheses denoting the points to which they refer,

$$(C) = -CC_1 \cos DCA \sec \delta$$
$$(C') = -C'C'_1 \cos D'DB.$$

The numerical values are

$$(C) = -0{\cdot}2706\Delta\omega,$$
$$(C') = -0{\cdot}3827\Delta\omega.$$

Similarly, we get for the other reference points DEF and their corresponding points

$$(E) = (C),$$
$$(E') = (C'),$$
$$(D) = (F) = +0{\cdot}3827\Delta\omega,$$
$$(D') = (F') = +0{\cdot}2706\Delta\omega.$$

If, by rotating plate A round its declination axis we bring C_1 into correspondence with C_1', the polar bearing of C_1' will remain unchanged, while the increment in the polar bearing of C_1 will have become

$$(-0{\cdot}3827 + 0{\cdot}2706)\Delta\omega = -0{\cdot}1121\Delta\omega.$$

E_1 will then have moved to E_2 and $E_1E_2 = C_1C_2$. But the increment in the polar bearing of E_1E_2 will be of contrary sign, and the difference in correspondence between E_1', which remains unchanged, and E_2 will now be

$$(-0{\cdot}3827 - (0{\cdot}2706 - 0{\cdot}1121))\Delta\omega = -0{\cdot}2242\Delta\omega.$$

Similarly, when D_1 and D_1' have been brought into correspondence by rotation of plate B round its declination axis the discrepancy between F' and F will also have become $-0{\cdot}2242\Delta\omega$.

Subject to instrumental and observational errors, these two discrepancies should be equal. The most probable value of $\Delta\omega$ is therefore

$$\Delta\omega = \frac{(E') - (E) + (F') - (F)}{0{\cdot}4484} = -2{\cdot}23\Delta\lambda.$$

Effect of Increment in the Polar Distance of a Plate on the Correspondence of Points.—An increment Δi being given to the polar distance of plate A, find the corresponding change in the polar bearing of a point C_2 (fig. 15).

From triangle P_1C_2S, in which $SP_1=\frac{\pi}{2}$,

$$\begin{aligned}\tan SC_2 &= \tan C_2P_1S \operatorname{cosec} P_1SC_2\\ &= \cot i \sec (i+u),\\ \cos SC_2P_1 &= -\cos C_2P_1S \cos P_1SC_2\\ &= -\sin i \sin (i+u),\\ \tan PC_2 &= \operatorname{cosec} C_2P_1S \tan P_1SC_2\\ &= \sec i \cot (i+u).\end{aligned}$$

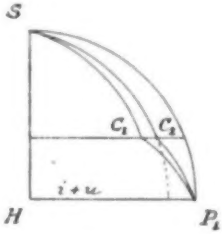

FIG. 15.

When a small increment Δi is given to P_1SC_2, C_2 moves along its parallel to C_1. Then, in triangle C_1SC_2, S being a small angle,

$$C_1C_2=\Delta i \sin SC_2,$$

and from triangle $C_1P_1C_2$, in which $\Delta\lambda$ is the small angle at P_1,

$$\Delta\lambda=-\frac{C_1C_2 \cos SC_2P_1}{\sin C_2P_1}=-\frac{\sin SC_2 \cos SC_2P_1}{\sin C_2P_1}\Delta i.$$

Numerically, for a reference point C in the position given before,

$$\Delta i=-3{\cdot}4144\Delta\lambda.$$

Influence of Errors in the Correspondence of Points on the Settings.—We are now enabled to determine the errors in the settings which result from

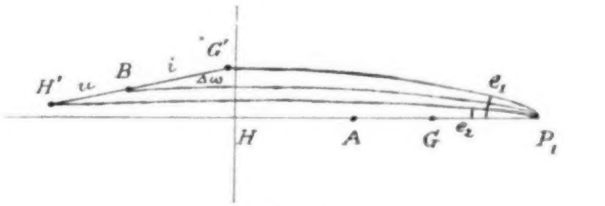

FIG. 16.

those made in the correspondence of the reference points. Beginning with the error in the difference of the position angles of the two plates, we will suppose an error e_1 to be made in placing G' in correspondence with G, and a similar error e_2 for H' and H, so that $G'=G-e_1$, and $H'=H-e_2$.

In triangle $H'G'P_1$ (fig. 16) we have

$$\frac{\sin (e_1-e_2)}{\sin (i+u)}=\sin G'H'P_1,$$

and in triangle $H'BP_1$,

$$\Delta\omega = \sin B = \sin H'P_1 \frac{\sin G'H'P_1}{\sin BP_1}$$

$$= 1{\cdot}307(e_1 - e_2).$$

From triangle BP_1H' we get

$$\sin BP_1H' = \frac{\sin u}{\cos(i+u)}\Delta\omega.$$

The error in (AB) is therefore

$$BP_1H' + e_2 = \frac{\sin u}{\cos(i+u)}\Delta\omega + e_2 = \tfrac{1}{2}(e_1 + e_2).$$

The effect of the errors e_1 and e_2 on (CC') and (EE') is

$$+0{\cdot}3827\Delta\omega + \tfrac{1}{2}(e_1 + e_2) = e_1,$$

and on (DD') and (FF'),

$$-0{\cdot}2706\Delta\omega + \tfrac{1}{2}(e_1 + e_2) = +0{\cdot}1465e_1 + 0{\cdot}8535e_2.$$

When C' is brought into correspondence with C by rotation of plate A round its declination axis, an error e_3 made in (CC') will be transmitted to (EE'), making the latter error

$$e_1 - e_3 + e_4,$$

where e_4 is the error made in setting E' into correspondence with E.

Similarly when D' is brought into correspondence with D, the error e_5 then made is transmitted to (FF'), making the latter error, after F' has been brought into correspondence with F with an error e_6,

$$+0{\cdot}1465e_1 + 0{\cdot}8535e_2 - e_5 + e_6.$$

If ϵ is the mean error of a single correspondence, the terminal *m.s.e.* for either (FF') or (EE') is therefore very nearly

$$\epsilon\sqrt{3} = 1{\cdot}732\epsilon,$$

and the *m.s.e.* of the correction $\Delta\omega$ to the position angles of plates A and B is, from a single terminal discrepancy,

$$\frac{1{\cdot}732}{0{\cdot}2242}\epsilon = 7{\cdot}73\epsilon,$$

and from the mean of the two discrepancies

$$\frac{7{\cdot}73}{\sqrt{2}} = 5{\cdot}46\epsilon.$$

We shall now proceed to consider the errors in the declination settings. We had for the relative errors in correspondence (CC') and (DD'),

$$(CC')=e_1+e_3$$
$$(DD')=+0{\cdot}1465e_1+0{\cdot}8535e_2+e_5,$$

their difference $(CC')-(DD')$ being

$$0{\cdot}854e_1-0{\cdot}854e_2+e_3-e_5.$$

The error made in the difference in declination of A and B will then be

$$-3{\cdot}414(0{\cdot}854e_1-0{\cdot}854e_2+e_3-e_5).$$

The sum of the squares of the coefficients of e is 3·457. The *m.s.e.* of the difference in declination of A and B is therefore

$$3{\cdot}414\sqrt{3{\cdot}457}\epsilon=6{\cdot}35\epsilon.$$

The total error in correspondence of (CC') will be the sum of the relative error $(CC')=e_1+e_3$ and of the terminal error (EE'), namely $2e_3-e_4$. Similarly, the total error in correspondence of (EE') will be $2e_5-e_6$, and the *m.s.e.* of either declination

$$3{\cdot}414\sqrt{3}\epsilon=5{\cdot}91\epsilon.$$

To sum up, the errors in the settings of either plate are :

	Total.	Relative.
Errors in position angle . . .	$5{\cdot}35\epsilon$	$1{\cdot}85\epsilon$
Errors in polar distances . . .	5·92	6·35
Errors in polar bearings . . .	0·70	0·70

If the correspondence in the polar bearings could be effected with the precision that was attained for correspondences in vertical planes with the author's measuring stereoscope,* the probable error of a correspondence would be $\pm0{\cdot}27\mu$ for a mark of best definition, and from $\pm1{\cdot}02$ to $2{\cdot}65\mu$ for ordinary topographical points, according to their character and definition. This is equivalent to angular errors of $\pm0{\cdot}4''$, $\pm1{\cdot}5''$ and $\pm3{\cdot}9''$. But in the former case instrumental errors were eliminated very completely by referring the measures differentially to a réseau. On the other hand, in the present case, groups of points may be substituted for single points, without adding materially to the labour of the observations, by simply taking the mean of a number of readings for different points, instead of a single reading, when determining each setting for correspondence.

For a probable error of $\pm2''$ in a correspondence, those in the settings would be

	Total.	Relative.
Position angles	10·7″	3·7″
Polar distances	11·8	12·7
Polar bearings	1·4	1·4

* B.A. Report, 1905, p. 322.

Mapping Attachment.—The mapping attachment is represented diagrammatically by fig. 17 and more fully in fig. 18. The plane of two rods *AB*, hinged together at *C*, rocks about an axis *MN* parallel to the polar axis of the machine. By means of a connecting rod *D* the plane of the rods is coupled to the pair of photogoniometers, the plane through the polar axis and the centre of the right-hand plate being set at a constant angle $90°+\theta$ with the plane *ABC* of the rods. *A* and *B* slide through two sleeves which are pivoted in the line *MN*. The length of *EF* may be varied by moving *F* along *MN*.

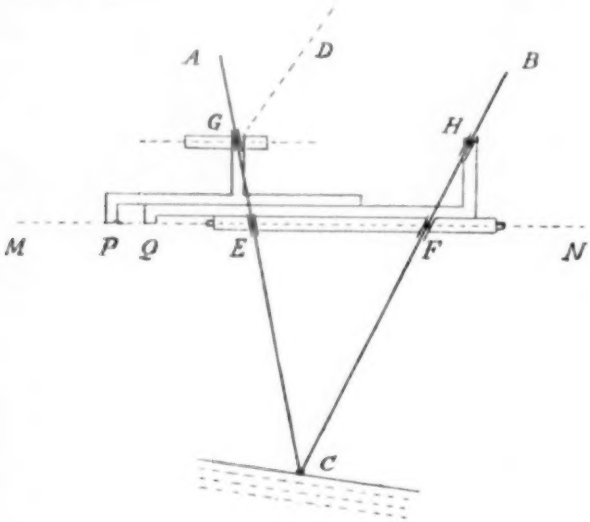

Fig. 17.

The rods *AB* also slide through two other sleeves *GH*, kept at a constant distance from *MN*, equal to *fg* of fig. 3, by two sliding callipers which transmit the motion of *G* and *H* to the points *P* and *Q* in the line of *MN*.

If, now, *P* and *Q* are connected by distance rods to the two mirror carriers, and the rods so set that *AC* is perpendicular to *MN* when *da* of fig. 3 is perpendicular to the polar axis, and *BC* is also perpendicular to *MN* when *d'a'* is perpendicular to the polar axis, the angles *aPN* and *a'QM* of fig. 3 will always be respectively equal to the angles *NEC* and *MFC* of fig. 17. The rotations of the pair of photogoniometers and of the plane of *ABC* being equal, it follows that if the optical index is kept on the surface of the optical model, the point *C* will trace in space a copy of the optical model to

any scale, within the range of the apparatus, determined by the ratio of the length of *EF* to that of the air base.

If, on the other hand, *C* is kept on a plane and the optical index on the optical model, *C* will describe a section of the model by the plane. When the plane is set at the inclination of the base the section will be a contour line. By displacing the plane parallel to itself any other contour

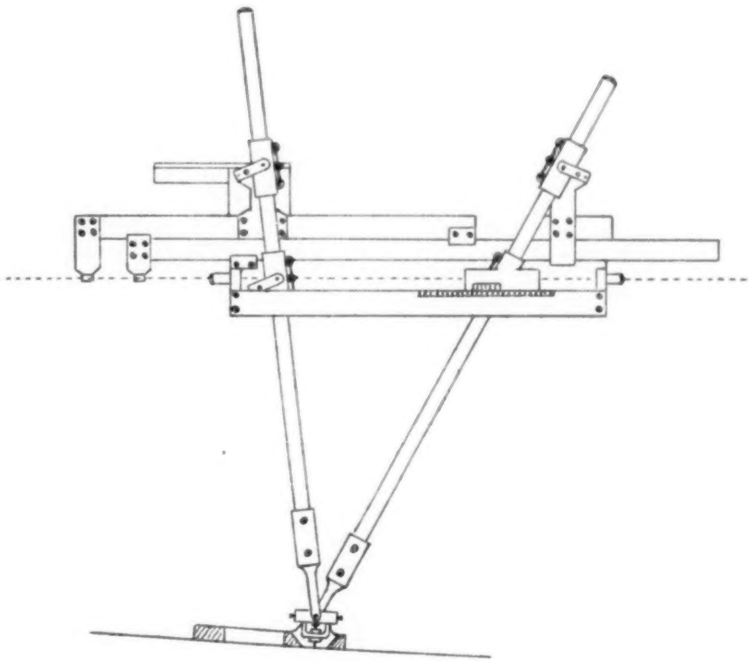

FIG. 18.

line may be drawn, or by using a height wheel actuating the plane simultaneously with the tracing of the features the map projection of any line of the optical model may be drawn.

The accurate working of the mapping attachment will depend largely upon the freedom from flexure of its moving parts and the absence of play in the joints, as also the observance of strictly "geometrical" principles in the design of the axes and slides. The first condition is rendered easy of attainment by the fact that the force required to work the moving parts of ths stereogoniometer may be made very small. The photogoniometers

rotate together round their common polar axis and can therefore be balanced accurately, while the only other parts of the stereogoniometer to which motion is imparted are the mirror carriers and their mechanism, which can be made of light weight. What friction remains may be reduced sufficiently by the introduction of ordinary devices such as are used to relieve the pressure of the pivots in a transit circle.

It is hoped that the second condition will also be satisfied by making the joints consist of selected steel balls connecting, at a determinate pressure, pairs of parts in which trihedral cups are formed. If the balls appertaining to any one movement are arranged to remain nearly in a plane, any small lateral departure will not affect the accuracy of the movement or introduce greater stiffness in the joints.

It should also be noted that owing to the large vertical angles used in the present method, the accuracy of the mapping mechanism need not be so great as in the case of ground stereoscopic surveys depending on small bases.

The further description of mechanical details will best be left over until the construction of a working instrument has been achieved. Other points not considered in the present paper, such as the adjustment of the apparatus, can then also be more suitably dealt with.

Witte Els Bosch,
May 1926.

[My thanks are due to Lieut. M. Hotine, R.E., of the Ordnance Survey, for correcting the proofs of the foregoing papers.—H. G. F.]

THE CHOROLOGY OF THE HETEROSOMATA OF SOUTH AFRICA, WITH SOME RELATIVE PROBLEMS.

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(With Six Charts.)

During a recent review of this sub-order of Fishes I was struck by the similarity which existed between certain of the South African species and those recorded from certain other seas, while a large number of species occurring in South African waters were endemic or peculiar to our seas. In view of this fact, the various localities of all the known species of South African Heterosomata were recorded on the accompanying sectional charts, so that their relative positions may readily be seen, and it is my intention to discuss, in the present paper, some of the main features appertaining to marine distribution in general and the distribution of the Heterosomata of South Africa in particular. For the sake of convenience the paper is divided into two parts:

Part I, dealing with the Oecology or Environment, the various Means of Dispersal, and other important features.

Part II, dealing with the Chorology, or Distribution in Space, as recorded on the accompanying charts.

PART I.

In the distribution of terrestrial animals we find that certain barriers, such as high mountains, barren tracts, and wide stretches of ocean, may form a permanent obstacle to the dispersal of a species. A good example is afforded by the Tasman Sea, which forms an impassable barrier to the passage of all animals, except strong-flying birds, between Australia and New Zealand.

In dealing with marine fauna, on the other hand, and especially the free-swimming types, we find that no such physical barriers to their distribution exist, for the watery medium is everywhere continuous and very many types have a wide range. The result of this absence of barriers is that there are

fairly large areas of the sea-bottom where a moderately uniform fauna exists.

Although mechanical barriers are practically non-existent, we find that barriers to the universal distribution of marine animals are, however, formed by the different types of structure evolved by them. Most types have developed a body-structure in conformity with their environment, which structure would restrict them to definite areas of the sea-bottom.

Coming to the Heterosomata, we find that during the course of evolution they have evolved the habit of lying on the left or the right side of their body on the sea-bottom, either in shallow or deep water, this habit leading to the animal living an almost sedentary life and having a somewhat limited range of movement. This limitation, however, is partly compensated for by the ability of the flat-fish to reproduce a free-swimming, bilaterally symmetrical, larval form. This larva lives for a time a pelagic existence amongst the plankton, drifting over relatively large areas. Ocean currents, on account of their ceaseless motion, afford a means of dispersal for these larval forms stronger than any agency provides on land. The larvae are so small, and their specific gravity so near that of the sea, that they are carried for great distances, and may finally settle down far away from their birthplace. The eggs of most of the Heterosomata are provided with an oil-globule and are, therefore, planktonic, and are drifted about passively in the sea by such agencies as tidal streams, winds, and currents. In these cases the only factor which limits the distance of dispersal is to be sought in the fact that a larval form has only a limited period of free-swimming existence, and, when metamorphosis takes place, it must assume the form of its parents and settle down on the bottom of the sea. In the case of fishes such as, *e.g.*, the snoek (*Thyrsites atun*), etc., which throughout their lives lead a free-swimming existence, we find that a wide range of distribution is more prevalent, since the larval form simply adopts the free-swimming mode of life of its parent and can cover great distances. Then, when the larva develops into the adult form, there is no change in its mode of life. In the case of flat-fishes it is clear that if the larval period lasted long enough there would apparently be no limit to the distribution of the species. It is obvious that the reason for the production of free-swimming larval forms is to increase the area of distribution of the species, for if such were not the case, the original " home " of such a species would soon become too small for the increase in the number of offspring and would lead to wholesale extermination. One need only examine, in connection with this, the fecundity of the turbot, which spawns nine million eggs yearly, to see the need for some means of dispersal of the species. The fecundity of many of the Heterosomata is probably due to the fact that so many of the larval forms must fail to find their proper habitat at the metamorphic period.

The distribution of the Heterosomata is evidently dependent upon certain factors which tend to widen their range on the one hand or to restrict it on the other.

FACTORS OF DISTRIBUTION.

In connection with the factors of distribution, we may divide them into

(*a*) Those factors which aid in the distribution or dispersal of certain species; and

(*b*) Those factors which retard or limit the distribution of other species.

It must be borne in mind that these factors are to a certain extent interrelated, and in some cases a factor tending to aid the distribution of one species may retard that of another species, while certain factors cannot act without the co-operation of others. They are apparently complementary.

(*a*) FACTORS AIDING DISTRIBUTION.

I. *Ocean Currents.* (See Chart I.)

It is evident from what has already been said that the chief of these factors is the means of dispersal provided by ocean currents, and in this connection it will be well to examine the nature of the currents around the South African coast.

The west coast of South Africa is washed by the Atlantic Ocean, the south and east coasts by the Indian Ocean. On the east we find the whole mass of water, owing to there being no outlet towards the north, is turned down the South African coast, where it successively forms the Mocambique, Natal, and Agulhas current. This current washes the east and south coasts down to Cape Point. It is essentially a warm-water current. The Antarctic Drift is partly deflected northwards along the west coast as the cold Benguela current, which passes along the coast up to the equator, where it is turned westwards along the equatorial line. Reaching the eastern projection of South America, it is divided into a portion, the Brazilian current, which passes southwards along the Brazilian coast, and another portion passing northwards through the Caribbean Sea into the Gulf of Mexico and becoming connected with the Gulf Stream, a part of the North Atlantic current.

Thus the sea around the South African coast exhibits an almost unique character in its oceanic circulation, since on the one hand it is connected by currents with the seas of the East, *i.e.* directly with the Indian Ocean and indirectly with the Pacific, while on the other hand it is connected with the South Atlantic Ocean by the deflected Antarctic Drift and also to the

North Atlantic, since a part of the Benguela current passes over through the Caribbean Sea to the Gulf of Mexico and thence to the North Atlantic.

With regard to the connection, direct or indirect, of the South African seas with the Indian Ocean and the Pacific, it is interesting to note that certain species of Heterosomata occurring in the Indian Ocean and/or in the Pacific have been found on the east coast of South Africa. These cases are fully described in Part II of the present paper, but reference may be made to *Cynoglossus lida*, first described from the coasts of India, the Malay Archipelago and Burma, and recently recorded from Durban. Then also *Lambdopsetta kitaharae* was first described from Kugoshima, Japan, and during the recent Marine Biological Survey was found off the Natal coast. In Part II the part played by ocean currents in the wide-range distribution of *Scaeops grandisquama* is discussed, and may be extended to the above-cited examples. It may be taken for granted that the currents play a great rôle in the wide-range distribution shown by *Solea turbynei*, this species being recorded from all the divisions of the South African coast. In this case we may record the fact that, by means of drift-bottles, it was shown (Gilchrist (3)) that some of the Agulhas current passes round Cape Point and up the west coast. To this fact, coupled with the proof afforded by a drift-bottle which was liberated west of Cape Point and subsequently found on the coast of Pernambuco, South America (Gilchrist (3)), that the Benguela current is capable of transferring a floating object from the South African coast across the Atlantic, we may look for the solution of the problem raised by the occurrence of *Limanda beanii* off the Natal coast and in the Gulf of Mexico. A parallel case is afforded by the distribution of *Peristedion gracile*, Goode and Bean (Gilchrist and von Bonde (16)), which is recorded from the same localities. In connection with these widely apart localities, we may note the occurrence of the deep-sea species *Melanostigma gelatinosum*, Günther (Gilchrist and von Bonde (16)), off the east coast of North America and the west coast of South Africa. Then there are the parallels to the occurrence of the same species off our east coast and in Japanese seas. There are many cases afforded by Fishes, *e.g. Parabembris curtis*, found off Natal and in Japanese seas. In connection with the Coelenterates, we find an Alcyonarian, *Euplexuara parciclados*, recorded from the west and south coasts and from Japan (J. Stuart-Thompson (13)).

Although currents play a considerable rôle in the distribution of certain species, it would appear as though some forms are affected by differences in temperature brought about by the meeting of a warm and a cold current, such as we find off Cape Point, where the Agulhas current is met by the colder Benguela current. This would cause a limitation to the distribution. Such cases are discussed under Temperature.

II. *Oecology (Environment).*

It is obvious that environment only acts as a factor of dispersal of species with habits such as those of the Heterosomata, when the "oikos" of the species becomes overcrowded, for it is only under such circumstances that the migratory tendencies of species would become developed and they would then set out in search of a new home with similar environmental features, for it is the environment, the condition of the home, the "oikos," which decides the tenants.

The dispersal provided by currents is to a certain extent restricted by environment, for the chances are against an animal continuing to flourish if it were to settle down in an environment different from that of its parental home, unless the animal in question can adapt itself to the new surroundings. Environment, however, may cause a wide distribution, as will be seen subsequently.

Just like with other faunas, the character of marine fauna is determined by its environment, and so the key to the character of the South African Heterosomata is probably to be found in the peculiar features of our seas. Several factors, the chief among which are the nature of bottom, presence or absence of vegetable life, etc., go to constitute the environment of a marine animal. In Part II the various localities of the species are stated and the nature of the bottom at each locality is given, as recorded in Reports Nos. 1 and 2 of the Fisheries and Marine Biological Survey for 1920 and 1921.

In studying the distribution of the South African Heterosomata with special reference to the nature of bottom on which they occur, one is struck by the fact that mud, sand, or shells, or a bottom composed of any two or all three, forms the chief component of the locality from which the flat-fishes are recorded. Taking as an example of Discontinuous Distribution the case of *Cynoglossus gilchristi* (No. 46), we find that it occurs on the east coast, north of lat. 30°, on a bottom composed in all cases of mud with or without shells or sand. On the west coast its localities are widely separated from the eastern ones, but we find the chief component of the bottom is mud or green mud. This is significant, for the distribution must have been effected by the ocean currents, and the environment, in which the nature of the bottom played a great part, evidently determined the range of the species. Other examples may be found by reference to Part II.

Environment may also be the cause of restricted distribution of certain species, cf. *Pseudorhombus natalensis*, when the conditions in the sea are optimal, *i.e.* when the conditions of temperature, depth of water, salinity, and sunlight are most favourable. The conditions on the east coast seem to be most favourable to this species and to most others, with the result that it is an exclusively east-coast form.

Johnson (5), in discussing the movements of a marine animal, assumes the existence of consciousness in it, and assumes that in a fish, just as in ourselves, consciousness has become an effective factor in evolution and behaviour. He draws the conclusion, from these assumptions and from the assumption of a quality of memory on the part of the animal—perhaps a kind of unconscious memory—that an animal will react not entirely in response to the stimulus which reaches it from without, but also in response to all the stimuli which have affected it in the past: that is, its behaviour at any time is modified by experience. He sums up his conclusions thus: "Now, if anyone attentively studies the facts of migration, it seems that this way of looking at them is more in accordance with what one sees than simply to suppose that the behaviour is a series of inevitable responses to changes in the environment."

(*b*) Factors Retarding or Limiting Distribution.

I. *Form of Body.*

As already stated, the barriers to the universal distribution of marine species are chiefly due to the fact that different types of structure are evolved by them, and, during the course of evolution, a specialisation in the feeding habit is acquired. In the case of the Heterosomata, the body-structure evidently affords the greatest factor in the process of limiting their distribution. It is probably on account of this that we find the majority of the South African Heterosomata are endemic, and many are restricted to definite areas. *Pseudorhombus natalensis* affords a good example of this. This species occurs very abundantly off the Natal coast, and at Station 190 as many as 250 specimens were procured.

II. *Temperature.*

The temperature of the sea is another important factor. From an examination of the species recorded in Part II, under the heading of "Species Endemic to South Africa," it will be seen that only two show a wide range. From the above-described character of the seas round the South African coasts, it will be seen that the east coast may be regarded as having a warmer temperature than the west coast. It has been found that the east-coast current gradually cools as it proceeds southwards and westwards, and that there is a very marked difference between the temperature of the water in False Bay and Table Bay. This difference was found to be as much as 6° in the summer (Gilchrist (2), and Juritz (9)).

It appears, therefore, as though only three out of a total of fifty-three species can adjust themselves to life in both seas, for *Cynoglossus gilchristi* is only recorded from the east and west coasts and must be placed in this category, the three species, therefore, being *Solea turbynei*, *Areliscus capensis*, and *Cynoglossus gilchristi*.

On the other hand, we may regard some species as cold-water species, and under this heading we find only two occurring exclusively on the colder west coast, viz. *Solea cleverleyi* and *Synaptura microlepis*. The remaining species are undoubtedly warm-water species, and we find that forty-six are recorded from the south and east coasts. Of this number, the majority are not found south of lat. 30° 10′ S.; but an interesting case is seen in *Cynoglossus ecaudatus*, which has been found only in shallow water off the Natal coast and in deep water south of Cape Point. A similar distribution has been recorded by Dr. K. H. Barnard, M.A., in connection with his work on the crustacean distribution. The Mocambique current is deflected by the Benguela current just at about this point, so that this species definitely shows warm-water affinities. In this connection it seems that temperature plays an important rôle in the dispersal afforded by currents, for the distribution is limited to the track of the Mocambique current.

Temperature also plays a part in the rate of development of an embryo. It has been calculated that if the temperature is reduced by 10° C., the time required for hatching out is increased about three times (Johnson (5)). Thus, the colder the water is, the longer will the period of development be; hence the embryo and larval form may be carried a longer distance by the currents before the metamorphic period is reached if the egg were laid in cold water than it would if it were laid in warmer water. This evidently will aid the distribution of a species, for, as the species migrated from warm to colder waters, the larval period (during which period the larva is almost entirely dependent on the ocean currents for its movement) is longer and the distance travelled is greater, so that the larva finally comes to settle down some distance away from its parental home. The progeny of this larva again repeat the same process, and so the species spreads gradually more and more. It is probably in this direction that an explanation of the wide discontinuous distribution of forms such as *Limanda beanii* must be sought.

III. *Salinity, etc.*

Salinity may also account for the limiting of distribution. In a series of observations carried out on board the S.S. *Pickle* during 1920–1921, it was found that the total salinity points per 1000 calculated from samples of sea-water taken at various places on the coast varied from 36·49 to 36·89. On the east coast generally the salinity was higher than on the west coast,

where it fell to 36·09 at certain points. The region off the Natal coast, whence the greatest number of Heterosomata was recorded, was found to have the highest salinity point, viz. 36·89 (Juritz (9)).

There is reason to believe that Fishes can detect the change in the salinity of sea-water by means of their taste-buds, and a change in the salinity of the water would probably cause a reaction on the part of the fish, so that it will search for a readjustment of its surroundings.

Another factor of some importance taken in conjunction with salinity is the hydrogen ion concentration, or shortly, the *pH*. During the recent voyage of H.M.S.A.S. *Protea*, it was found that the *pH* of the Cape seas was greater than that of the Natal seas,* *i.e.* the waters of the Cape were much less acid than those of Natal. It is noteworthy that, as far as the Heterosomata are concerned, although some have a wide South African distribution, the majority of species are recorded from the east coast, and it would appear from this that the *pH* plays some part as a limiting factor.

With regard to *pH*, Powers (12) states: "The ability of fishes to withstand wide variations in the range of *pH* concentration of the sea-water can be correlated with their habitats. The fishes that are most resistant to a wide variation in the *pH* concentration are most cosmopolitan in their habitat. Those that are least resistant to a variation in the *pH* concentration are the most restricted in their range of habitat. It is suggested that the variation in the ability to absorb oxygen at low tension at a given *pH* of individuals of a species is dependent upon the alkaline reserve of the blood of the individual fish."

As a general rule, the limiting factor for animals appears to be the quantity of food present, but under some unusual conditions oxygen may become the limiting factor. Fish in an aquarium, open to the air and with a constant stream of oxygenated sea-water flowing in, suffocated if the stream of water is not sufficiently rapid. The same is true of sponges and other animals. An experiment was carried out on these lines (M'Clendon (7)), and it was found that if the lowest oxygen concentration found right at the sea-surface was taken, 1 kg. of fish would use all the oxygen in 4300 litres of sea-water in 24 hours, and would show symptoms of altered metabolism before it was used up. Oxygen diffuses into the water from the air very slowly, and the fact that fish can come to the surface does not help them much. It seems improbable that fish would congregate in such numbers as to suffocate, hence this oxygen factor may cause the dispersal of species in order to obviate overcrowding.

* I am indebted to Mr. W. J. Copenhagen for these facts.

Comparison with Other Fauna recorded from South African Waters.

Such a comparison may conveniently be stated in tabular form as follows :—

	Total No. of Species.	Depth.	Endemic.	Indo-Pac.	Atlantic.	Austral.	Cosmop.
Heterosomata	53	Shallow water 38	31	2	1	..	4
		Deep water 15	10	1	2	..	2
Echinodermata	184	Littoral 86	45	34	3	2	2
		Abyssal or continent 98	55	6	15	12	10
Alcyonaria .	98	..	65				
Mollusca .	Majority of littoral species are endemic						

From this table it will be noticed that the Heterosomata agree closely in their distribution with the other groups enumerated above in having

(*a*) The majority of the species endemic.

(*b*) Few cosmopolitan species.

It must be noted, however, that of the four shallow-water cosmopolitan species all have been recorded from Indo-Pacific localities, while one has in addition also been recorded from Austral regions. The deep-sea one is recorded also from the Atlantic and Mediterranean.

It would appear, therefore, as though the shallow-water forms have come from the East, while the deep-water form came from the West. H. Lyman Clark (14) records a similar condition for the Echinoderm fauna : "The littoral Echinoderms of South Africa seem to have come from the East, but with the passage of time have become very largely specifically differentiated. Additions from the West have been so exceptional as to be conspicuous.

"It appears that the deeper-water fauna of the Cape region has not

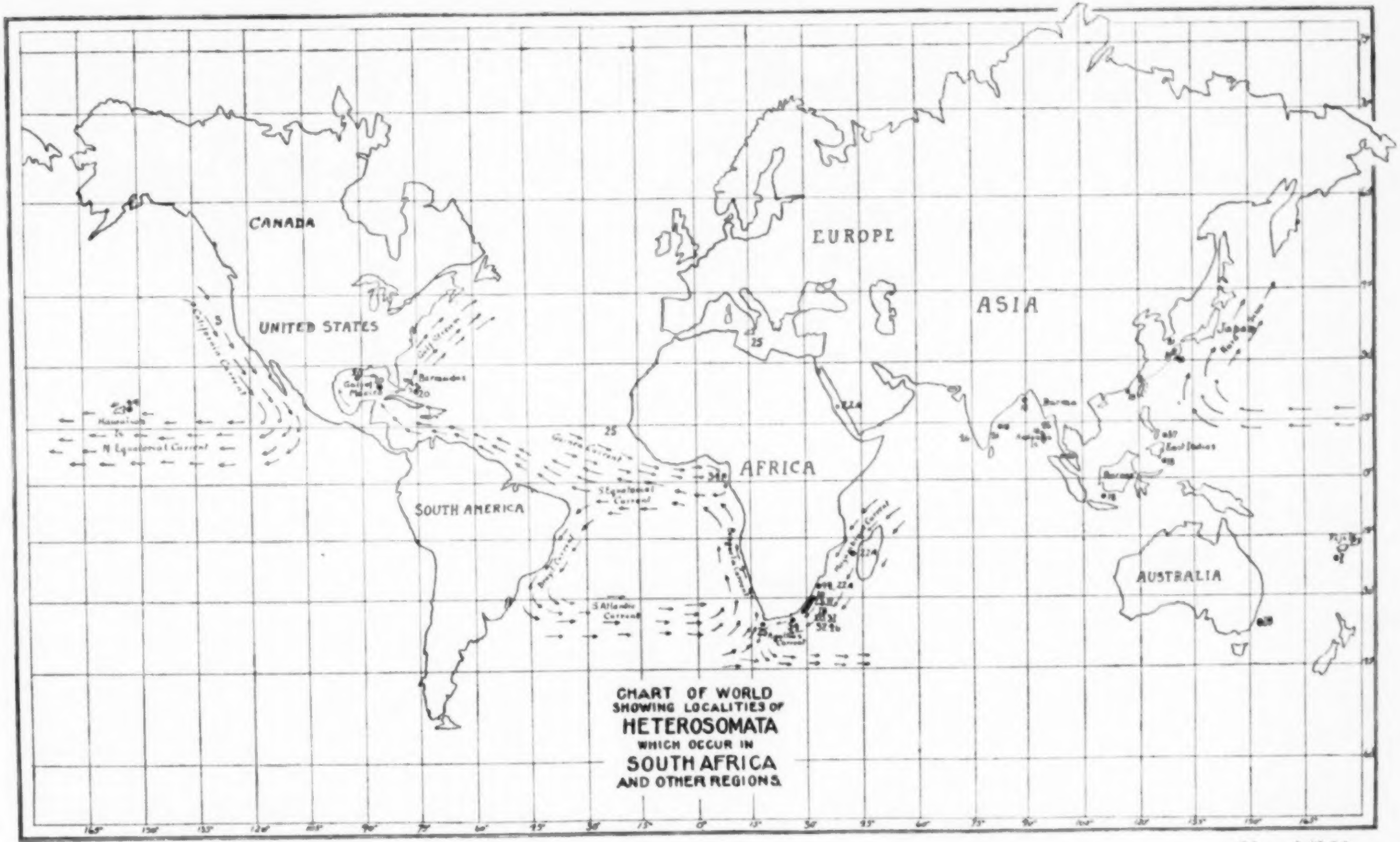


Chart No. 1.

1. *Platophrys pantherinus.*
3. *Scaeops grandisquama.*
10. *Etropus remosus* (from Atlantic). *Etropus* sp. (from Natal coast).
11. *Lambdopsetta kitaharae.*
18. *Pseudorhombus russelli.*
20. *Limanda beanii.*
22A. *Pardachirus marmoratus.*
25. *Solea impar.*
31. *Aesopia cornuta.*
34. *Synaptura punctatissima.*
37. *Plagusia marmorata* (from East Indies). *Plagusia marmorata*, var. *africana* (from Natal coast).
46. *Cynoglossus lida.*
49. *Symphurus strictus.*

come in from the East, but has largely come from the West and North, with the addition of a considerable Austral element, the significance of which is not clear."

With regard to the Alcyonaria, it is stated that in the southern area there is an Alcyonarian fauna peculiar to it, much more so than on the Natal coast. On examining the Heterosomata we find that the converse holds, for the Natal coast is much richer than the south or west coasts.

Sowerby (10) notes that a number of British and European molluscan species are found also on the South African coast. Tomlin (11) states that the "trend of the Atlantic currents should make us very chary of admitting palaearctic species to the South African list." This statement corresponds very well with what is found in the Heterosomata. Here there is not a single palaearctic species (except perhaps *Solea impar*, whose occurrence off the Cape of Good Hope is doubtful) occurring in South African seas.

In the case of the Mollusca we find that there is a large total of endemic species. Fischer (Jour. Man. Conch., p. 155) computes it as being 50 per cent. of the total number, but it is probably higher.

PART II.

In dealing with the CHOROLOGY of the South African Heterosomata it appears best to group the various species under three distinct divisions, as follows :—

I. Those forms which are ENDEMIC or native to our seas.

These species fall into three sub-divisions, viz. :—

(i) Those showing a WIDE RANGE of distribution, occurring on the west, south, and east coasts.

(ii) Those showing a LIMITED RANGE, occurring only on one of the three sections of the coast.

(iii) Those occurring on any two of the three divisions of the coast.

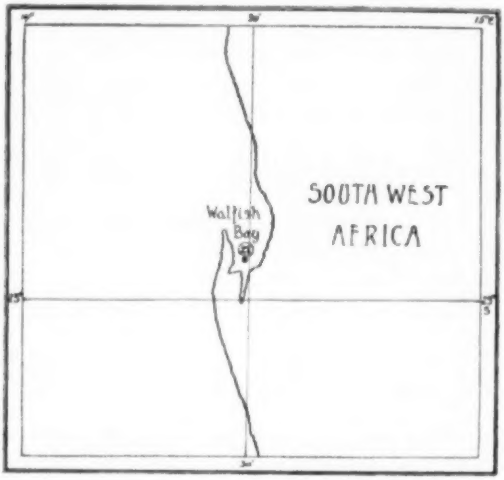
II. Those forms which may be taken as examples of a WIDE-RANGE DISTRIBUTION, *i.e.* they are known from our seas and extend to other localities. These may be looked upon as COSMOPOLITAN SPECIES.

III. Those forms which may be taken as examples of a DISCONTINUOUS DISTRIBUTION, *i.e.* they occur in our seas and are recorded from areas isolated from their South African localities by great tracts of sea.

In the following lists the number before each species is the same as the number on the various charts, and the locality from which a species was first recorded is marked thus (2).

As a basis of distinction the South African coast-line may be divided into three sections, the lines of demarcation being purely arbitrary :—

1. West Coast, extending from Walfish Bay to Cape Point.
2. South Coast, ,, ,, Cape Point to Algoa Bay.
3. East Coast, ,, ,, Algoa Bay to Delagoa Bay.



22. *Solea cleverleyi.*

I. Endemic Species.

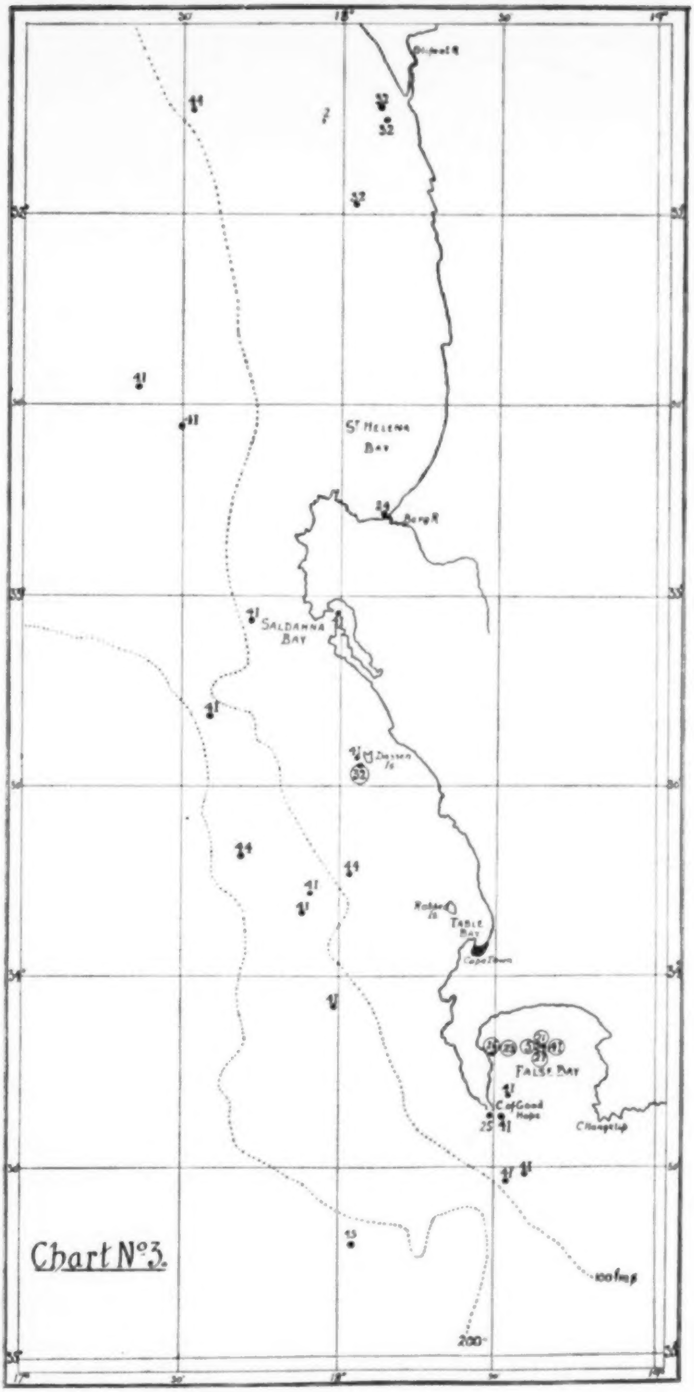
(i) *Wide Range. See Charts III, IV, V, and VI.*

24. *Solea turbynei*, Gilchrist.

This species is fairly common on the South African coast, being found in many localities from Delagoa Bay down the coast to Cape Point. On the west coast, however, it is apparently restricted to the Berg River. Here it occurs on a bottom composed of mud, whereas at the other localities the bottom is composed mostly of sand, or sand and shells. It is principally a shallow-water form.

41. *Areliscus capensis* (Kaup).

This species is fairly common on the west coast. It is found in False Bay and round the Cape of Good Hope. On the south coast the locality seems to be restricted to Algoa Bay, while on the east coast it was only



5. *Arnoglossus capensis.*
21. *Achirus capensis.*
23. *Solea capensis.*
24. *Solea turbynei.*
25. *Solea impar.*
26. *Solea simonensis.*
27. *Solea fulvo-marginata.*
32. *Synaptura microlepis.*
41. *Areliscus capensis.*
44. *Cynoglossus gilchristi.*
45. *Cynoglossus ecaudatus.*

found at a single locality, viz. at Station 180, off the mouth of the Umhlati River, in 28 fms., on a sandy bottom.

(ii) *Limited Range.*

(a) *Forms occurring only on the West Coast. See Charts II and III.*

22. *Solea cleverleyi*, Gilchrist.

Walfish Bay is the only locality recorded for this species, and only the type specimen has been procured. This species is apparently restricted to Walfish Bay.

32. *Synaptura microlepis*, Bleeker.

This species occurs on a stretch of ground between Dassen Island and Saldahna Bay and also further north. The bottom of all localities from which this species has been recorded is composed of mud.

The above two species 22 and 32 may be looked upon as purely cold-water forms, occurring only on the west coast.

(b) *Forms occurring only on the South Coast. See Charts III and IV.*

5. *Arnoglossus capensis*, Boulenger.

This species is restricted in its distribution, having only been found in False Bay, while a species of the same genus, viz. *A. macrolepis*, is peculiar to the east coast.

21. *Achirus capensis* (Kaup).

This is the only South African representative of the genus, and it is restricted to False Bay.

26. *Solea simonensis*, von Bonde.

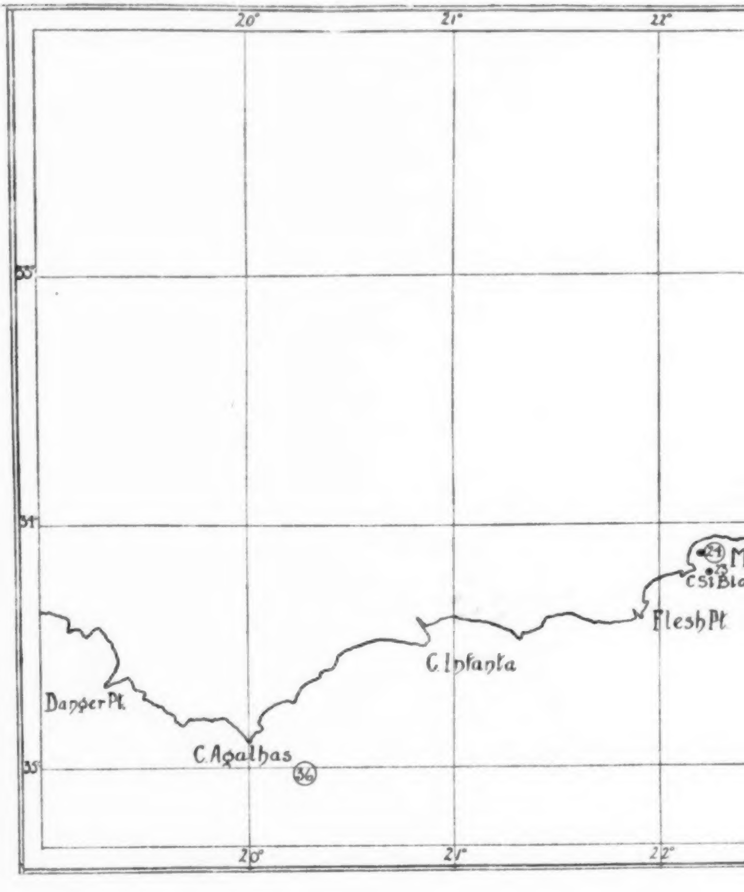
Only the type specimen has been found, its locality being Simons Bay.

27. *Solea fulvo-marginata*, Gilchrist.

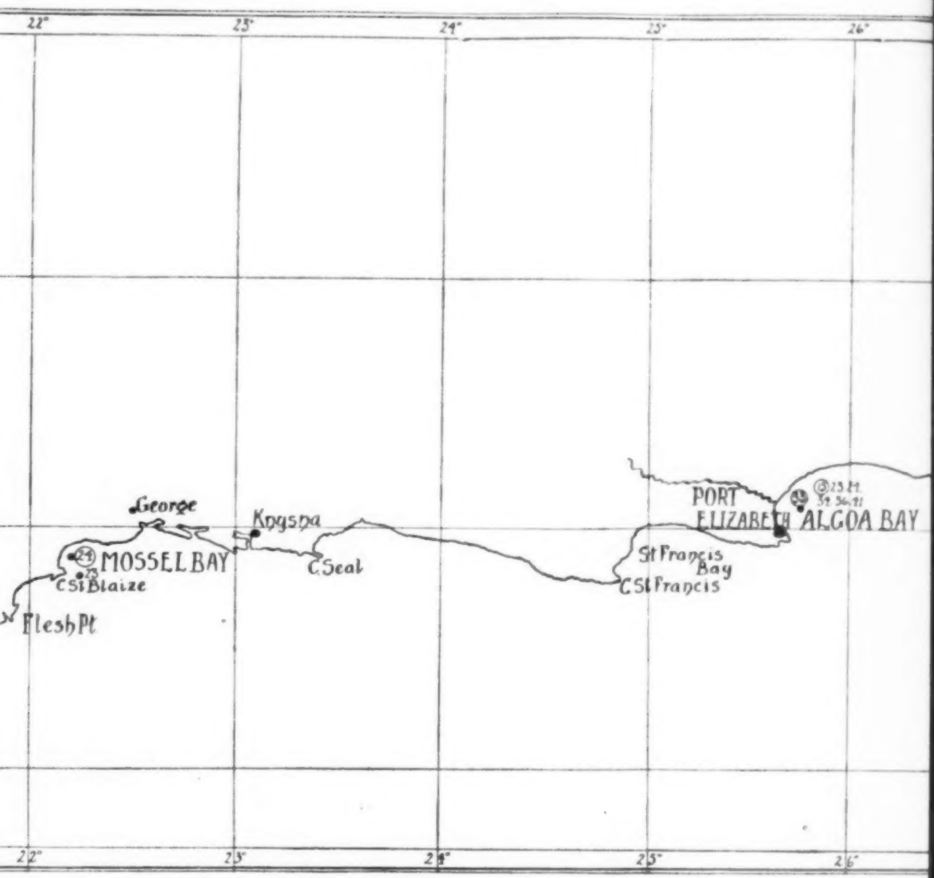
This species is occasionally taken by seine net in False Bay, to which region it is restricted.

33. *Synaptura marginata*, Boulenger.

Only the type specimen has been found, its locality being Algoa Bay, depth 22 fms.



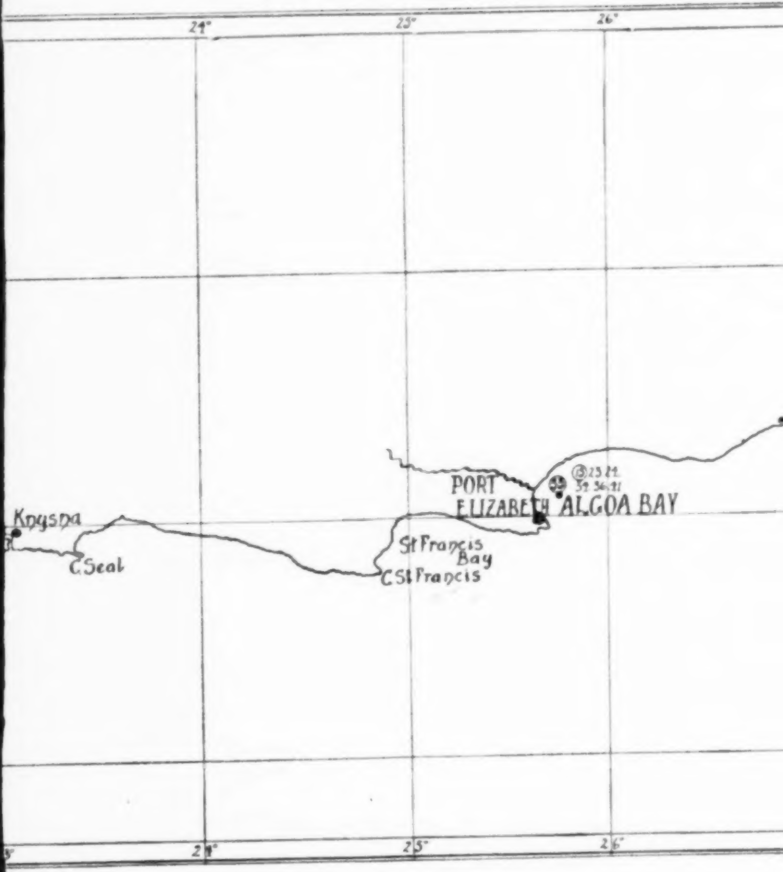
15. *Paralichthodes alg*
23. *Solea capensis.*
24. *Solea turbynei.*



alichthodes algoensis.
a capensis.
a turbynei.

29. *Solea melanoptera.*
33. *Synaptura marginata.*
34. *Synaptura punctatissima.*

36. *Austroglossus pectoralis.*
41. *Areliscus capensis.*
48. *Symphurus variegatus.*



29. *Solea melanoptera.*
33. *Synaptura marginata.*
34. *Synaptura punctatissima.*
36. *Austroglossus pectoralis.*
41. *Areliscus capensis.*
48. *Symphurus variegatus.*

[To face p. 126.

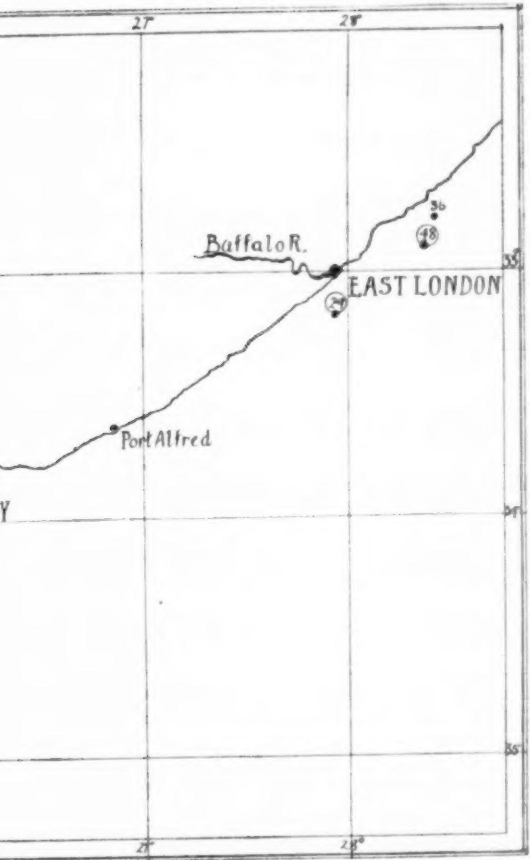
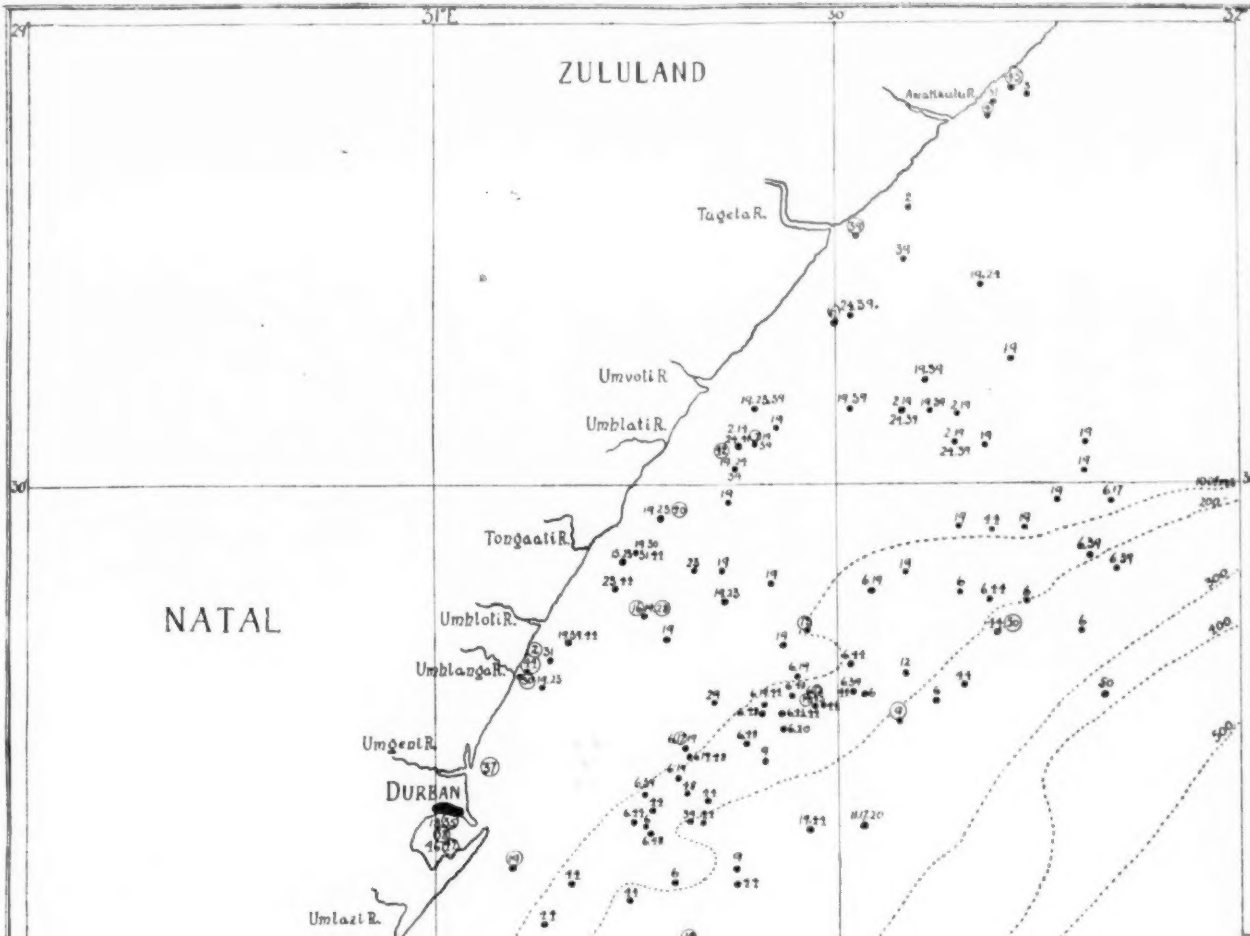
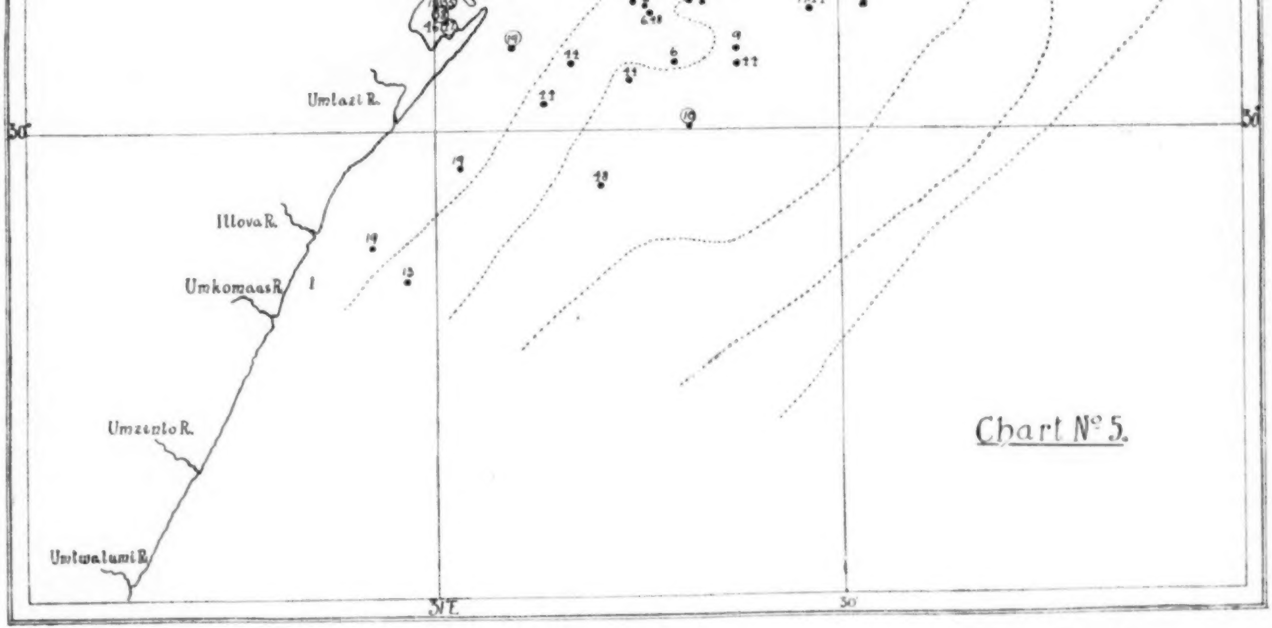


Chart No. 4.


ZULULAND
NATAL
Amatikulu R.
Tugela R.
Umvoti R.
Umhlali R.
Tongaati R.
Umhloti R.
Umhlanga R.
Umgeni R.
DURBAN
Umlazi R.
31° E.
30
29
32
100 fms
200
300
400
500



1. *Platophrys pantherinus.*
2 *Crossorhombus dimorphus.*
3. *Scaeops grandisquama.*
4. *Engyprosopon natalensis.*
6. *Arnoglossus macrolepis.*
7. *Trichopsetta dalgleishi.*
9. *Chascanopsetta maculata.*
10. *Etropus* sp.
11. *Lambdopsetta kitaharae.*
12. *Lambdopsetta pectoralis.*
13. *Laeops nigromaculatus.*
14. *Laeops microphthalmus.*
15. *Paralichthodes algoensis.*
16. *Samaris ornatus.*
17. *Poecilopsetta bicolorata.*
18. *Pseudorhombus russelli.*
19. *Pseudorhombus natalensis.*
20. *Limanda beanii.*
23. *Solea capensis.*
24. *Solea turbynei.*
28. *Solea quadriocellata.*
29. *Solea melanoptera.*
30. *Zebrias regani.*
31. *Aesopia cornuta.*
35. *Synaptura ciliata.*
37. *Plagusia marmorata*, var. *africana.*
38. *Paraplagusia robinsoni.*
39. *Cynoglossoides attenuatus.*
40. *Areliscus natalensis.*
41. *Areliscus capensis.*
42. *Areliscus microphthalmus.*
43. *Areliscus marleyi.*
44. *Cynoglossus gilchristi.*
45. *Cynoglossus ecaudatus.*
46. *Cynoglossus lida.*
47. *Cynoglossus durbanensis.*
48. *Symphurus variegatus.*
50. *Symphurus ocellatus.*

8. *Chascanopsetta gilchristi.*
17. *Samaris delagoensis.*
20. *Limanda beanii.*
22A. *Pardachirus marmoratus.*
24. *Solea turbynei.*
49. *Symphurus strictus.*
50. *Cynoglossus hunteri.*

(c) ***Forms occurring on the East Coast. See Charts V and VI.***

2. *Crossorhombus dimorphis* (Gilchrist).

This species was first recorded from the east coast, 2½ miles off the mouth of the Umhlanga River, from a depth of 22–26 fms.; nature of bottom, fine sand. Since then it has been found in more localities all having the bottom composed of sand, or sand and shells. It is apparently a shallow-water form.

4. *Engyprosopon natalensis*, Regan.

This species occurs off the mouth of the Amatikulu River, Natal, depth 26–27 fms., this being the only locality from which it has been recorded.

6. *Arnoglossus macrolepis*, Gilchrist.

This species was first recorded from the Tugela River, Natal, bearing north; distant 22 miles, depth 63–75 fms.; bottom mud. During the recent Government Survey it has been found in great abundance, mostly in deep water, the depths varying from 70 fms. to 212 fms. In all cases the bottom was mud, or mud with sand and shells. Although the original locality was near the Tugela River, no specimens were found in that vicinity recently, but the localities all lie between latitudes 29° 30′ and 30° S. In this area this species occurs very abundantly. It is interesting to note that a species of the same genus, *A. capensis*, is restricted to False Bay, on the south coast.

7. *Trichopsetta dalgleishi*, von Bonde.

Only two examples of this species have as yet been found on a bottom of black mud.

8. *Chascanopsetta gilchristi*, von Bonde.

Only a single specimen has as yet been found, the locality being off Portuguese East Africa, in deep water, bottom mud.

9. *Chascanopsetta maculata*, von Bonde.

This species, from the coast of Natal and Delagoa Bay, is apparently restricted to deep water.

10. *Etropus* sp., von Bonde.

This immature specimen was found in Natal waters in 220 fms., bottom mud. sand, and shells.

12. *Lambdopsetta pectoralis*, von Bonde.

A few specimens were procured from Natal and Portuguese East Africa in deep water, bottom mud in all cases.

13. *Laeops nigromaculatus*, von Bonde.

A specimen was procured from the Natal coast, east of the Umhloti River, in deep water, while twelve were procured from east of the Umkomaas River. Later some specimens were also procured from Delagoa Bay, the bottom in all cases being mud and sand.

16. *Samaris ornatus*, von Bonde.

Only the type specimen has been found in shallow water east of the mouth of the Umhloti River.

17. *Samaris delagoensis*, von Bonde.

This species, from Delagoa Bay, forms the second example of the genus *Samaris* found in South African waters.

17. *Poecilopsetta bicolorata*, von Bonde.

Ten examples were found at the Station 110, east of the Umgeni River mouth, in shallow water; two from Station 115, east of Durban, in deep water; and one from Station 468, east by north of the mouth of Tongaati River, in shallow water, all on sandy or muddy bottoms.

19. *Pseudorhombus natalensis*, Gilchrist.

This species was first recorded from "Cape Natal, bearing W. by N., distant 6½ miles, depth 54 fms.; bottom fine sand." Since then it has been found in abundance at various stations. It is apparently a shallow-water form, occurring mostly in depths from 25–100 fms. It is occasionally found in depths of 100–230 fms. As many as 93 specimens were procured in shallow water at a certain station, while only one was procured from the deep sea in 230 fms. It appears to occur in regions which may be demarcated by lines following the contour of the coast-line. At many stations it occurs along with *Cynoglossoides attenuatus*, while at others it was found along with *Solea turbynei*.

28. *Solea quadriocellata*, von Bonde.

The locality of this species is the same as that of *Samaris ornatus*.

29. *Solea melanoptera* (Gilchrist).

This species was originally recorded as *Synaptura melanoptera*, Gilchrist, from off East London, lat. 33° 6′ 45″ S., long. 27° 55′ 45″ E.; depth 43 fms.; bottom sand, shells, and mud. Since then only a single specimen has been recorded from a station on the Natal coast, the nature of bottom being similar to that of the original locality.

30. *Zebrias regani* (Gilchrist).

This species was originally found 2½ miles from the mouth of the Umhlanga River; depth 22–26 fms.; bottom fine sand. Since then nineteen specimens have been found further north, east of the Tongaati River, in 28 fms., bottom fine sand.

35. *Synaptura ciliata*, Gilchrist.

This species has only been recorded from the Inner Harbour, Durban, Natal.

37. *Plagusia marmorata*, var. *africana*, Gilchrist.

A single specimen was recorded from Natal.

It is significant that the species *P. marmoratus* is recorded from the East Indies, from which locality *Pseudorhombus russelli*, also found on our east coast and at other places, is also recorded. The above species closely resembles *P. marmorata*, Bleeker, and has been made a variety of this species.

38. *Paraplagusia robinsoni*, Regan.

This species has only been recorded from Durban, Natal.

39. *Cynoglossoides attenuatus* (Gilchrist).

This species was originally recorded from the Tugela River mouth, bearing N. by W., distant 4½ miles, depth 24 fms., bottom mud. Since then it has been procured at various other stations in varying numbers. Although it occurs in great abundance in shallow water, it is also abundant in deep water up to 160 fms. In deeper water it is not so abundant, only two being procured in 210 fms., while in 182 fms. only two were found. The nature of the bottom is in nearly all cases mud or sand and shells.

40. *Areliscus natalensis*, von Bonde.

Only two specimens have as yet been recorded from South Africa, both being from the Natal coast.

42. *Areliscus microphthalmus*, von Bonde.

This species was procured together with *Crossorhombus dimorphis*, *Laeops microphthalmus*, *Solea turbynei*, and *Areliscus capensis*. It has also been recorded from Portuguese East Africa.

43. *Areliscus marleyi* (Regan).

The original locality was given as Natal. Since then more specimens have been procured from two stations off the Natal coast in deep water and Delagoa Bay in shallow water.

47. *Cynoglossus durbanensis*, Regan.

This species agrees very closely with *Areliscus natalensis* (No. 40), except for the fact that the former has only two lateral lines on the eyed-side and none on the right side. During the Marine Survey none of these were recorded, and only two examples of *A. natalensis* were procured.

50. *Cynoglossus hunteri*, von Bonde.

Only a single specimen has been recorded, and it was obtained from Delagoa Bay.

48. *Symphurus variegatus* (Gilchrist).

The original locality was given as off the coast of East London (Buffalo River, bearing north, distant 15 miles), at a depth of 310 fms., where only a single specimen was procured. Since then a few specimens have been found at various stations, the largest number being seven from 171 fms. It is apparently a deep-sea form. The stations are very close together between lats. 29° 30′ and 30° S., bounded by long. 31° 30′ E. The bottom is similar in each case, being mud or mud and sand.

50. *Symphurus ocellatus*, von Bonde.

Only two specimens have been procured, one at each of two different stations fairly close together, the bottom being in each case composed of mud.

(iii) *Forms occurring on Two of the Three Sections of the Coast. See Charts III, IV, and V.*

15. *Paralichthodes algoensis*, Gilchrist.

This species was originally found in Algoa Bay. Since then another specimen was procured off the mouth of the Tongaati River, Natal, in

shallow water. It is not known from the west coast, occurring only on the east and south.

23. *Solea capensis*, Gilchrist.

This species was originally recorded from 4½ miles off Cape St. Blaize in 30 fms., bottom mud. It has been found in small numbers at other stations, three having been recorded from Station 194. Some specimens were procured from Fish Hoek and Muizenberg (False Bay). It is apparently a shallow-water form, and is known only from the south and east coasts.

36. *Austroglossus pectoralis* (Kaup).

This species occurs abundantly on the Agulhas bank off the south coast, and is also recorded from Algoa Bay. The former is probably the locality from which it was first recorded.

44. *Cynoglossus gilchristi*, Regan.

This species was originally recorded by Gilchrist (Mar. Inv. S. Afr., iii, p. 12, pl. xxx (1902)) as *C. brachycephalus*, from 2½ miles off the Umhlanga River mouth (Natal), in 22–26 fms., bottom fine sand. In his review of the Flat-Fishes of Natal (Ann. Durban Mus., vol. ii, pt. 5, p. 222), Regan changed the name of the species to *gilchristi*, owing to the name *brachycephalus* being preoccupied by Bleeker, viz. *C. brachycephalus*, Bleeker (Atl. Ichth., vol. vi, p. 38, pl. xiii, fig. 6).

This species is fairly abundant on the Natal coast, and is apparently a deep-sea form. It was procured in great numbers from a few shallow-water stations, viz. Station 190, depth 27 fms., 115 specimens. On the west coast it has been procured from three stations, all in 78–95 fms. The largest number was five from 78 fms., bottom mud. This species affords an interesting case of Discontinuous Distribution, as it does not occur at all on the south coast, but seems to be confined to the west and east. On the east coast it does not occur south of lat. 30°, while on the west coast it occurs as low down as lat. 33° 45′ S. This is a case of a species occurring in the warm Agulhas current and also in the cold Benguela current. It is significant that the nature of bottom of the stations on the west coast is similar to that of the east coast.

45. *Cynoglossus ecaudatus*, Gilchrist.

This species was originally recorded from "Amatikulu River mouth N.W. by W. ¾ W., 12 miles, depth 26–27 fms." It was also recorded from the south coast from Cape Point E. by N. ¾ N., distant 34 miles, depth

480–600 fms. It was not found in the recent survey. The above distribution gives another good example of Discontinuous Distribution, the former locality being on the Natal coast, lat. 29° 6′ S., and the latter on the south coast from lat. 34° 50′ S., long. 18° 15′ E. In the former case it is from shallow water, while in the latter it is from deep water. It is peculiar that the species does not extend along the west coast, being apparently restricted to the warmer Agulhas current of the south coast and east coast.

A similar case has been recorded by Dr. K. H. Barnard, M.A., in "The Distribution of Marine Crustacea in S. African Waters" (MS. 1924), viz. *Penaeus longicornis* and *Conchoecetes artificiosus*, occurring in the shallow waters of Natal and Zululand as well as in deep water (460–650 fms.) off Cape Point.

II. Cosmopolitan Species. See Chart I.

Those species recorded from three or more localities are grouped together under this heading.

It is noteworthy that the majority of the South African Heterosomata falling under this and the next division are distinctly related to those of the Indo-Pacific and Australian regions.

Five species may be looked upon as cosmopolitan in their distribution, and of these four show affinities with Japanese, Indian, or Australian species, while the remaining one has been described from the Mediterranean and north-west coast of Africa. It may, however, be added that the occurrence of this species, *Solea impar*, off the Cape of Good Hope is doubtful, since it has never been rediscovered.

3. *Scaeops grandisquama* (Schlegel).

This species was found off the east coast of Natal, Amatikulu River mouth, bearing N.W. by N. ¾ N., distant 12 miles, depth 26–27 fms., bottom mud.

It has been recorded from Wakanoura and Nagasaki, from Chinese and Japanese seas, and also from the north-west coast of America.

This distribution presents some peculiar features. In some instances our east-coast species correspond with certain species from Japanese waters, *e.g.* in the family Scorpaenidae, *Parabembris curtis*, Schlegel, a deep-sea fish, was recorded from Japan, while Regan recorded a specimen from the Natal coast. In the Heterosomata dealt with under this and the next division we find that certain of our species correspond to those of Japan. There is probably some connection between the currents of the Japanese seas and those of the Indian Ocean through the Straits of Malacca, so that

the connection between East African seas and the Indian Ocean may be extended to the Japanese waters. With regard to this, the distribution of *Pseudorhombus russelli* is interesting, as it follows a line from the east coast, through the seas and estuaries of India, to Japan and Australia.

As seen above, this species has also been recorded from the north-west coast of America. A study of the ocean currents may help in explaining this distribution. On the north-west coast of America we find the Californian current moving down the coast as far as lat. 20° N. There it is deflected westwards and meets the northern Equatorial Drift which crosses the Pacific at about the 10° N. lat. In the region of the East Indies this current is deflected northwards towards Japan and becomes the Kuro Siwo current. The variation in the temperature of the various currents would probably not be more than a few degrees. It is a moot point, therefore, whether the larvae of species reproducing on the north-west coast of America may be swept down the coast until they are nearing their metamorphic period, when they settle down at some distance from the parental home at a spot having a similar environment. The larvae may grow to adult forms which reproduce, their larvae again proceeding a distance from the breeding-place and then settling down. This process may be repeated, the larvae following the course of the current, until eventually the other side of the ocean is reached. The very fact that the ocean currents indirectly link up the north-western American seas with those of Japan, lends colour to this mode of dispersal. This explanation has, of course, some drawbacks, since the depth of the Pacific varies greatly between the two points in question, and one must not forget that the west coast of America is separated from Japan by 4750 miles. It would, however, prove to be strong evidence in favour of this view if specimens of this species were procured from the deep sea of the Pacific in the region of the above-mentioned currents.

Darwin (1) refers to the problem as to "whether species have been created at one or more points of the earth's surface," or whether species separated by many miles have "centres of creation." He says: "Undoubtedly there are very many cases of extreme difficulty in understanding how the same species could possibly have migrated from one point to the several distant and isolated points where now found. Nevertheless the simplicity of the view that each species was first produced within a single region captivates the mind. He who rejects it, rejects the *vera causa* of ordinary generation with subsequent migration and calls in the agency of a miracle. It is universally admitted that in most cases the area inhabited by a species is continuous: and when an animal inhabits two points so distant from each other, or with an interval of such a nature, that the space could not be easily passed over by migration, the fact is given as something

remarkable and exceptional." He shows how certain quadrupeds are common to both Europe and Britain owing to the former land connection, and then raises the important question, "Why do we not find a single mammal common to Europe and Australia or South America if the same species can be produced at two separate points?" The conditions of life are nearly the same, so that many European animals have become naturalised in America and Australia. To his question he gives this answer: "Mammals have not been able to migrate, whereas some plants have migrated across the vast and broken interspace. The great and striking influence which barriers of every kind have had on distribution is intelligible only on the view that the great majority of species have been produced on one side only, and have not been able to migrate to the other side . . . very many genera and a still greater number of sections of genera are confined to a single region (cf. *Pseudorhombus natalensis*, p. 9), and it has been observed that the most natural genera are generally local, or, if they have a wide range, that their range is continuous." He draws conclusions from this that "the view of each species having been produced in one area alone, and having subsequently migrated from that area as far as its powers of migration and subsistence under past and present conditions permitted, is the more probable," admitting, however, that many cases (of which we have the species *Scaeops grandisquama* and *Limanda beanii*) occur where it is almost impossible to explain how the same species could have passed from one point to the other. "The geographical and climatal conditions, which have occurred within recent geological times, must have rendered discontinuous the formerly continuous range of many species."

Hans Gadow (4) accounts for the discontinuity of range of certain species as either

(i) due to the fact that the respective faunas had a multiple origin and are instances of convergent evolution and where similar environmental conditions prevailed; or

(ii) in the case of respective blood-related animals, if they belong to the same genera or species, due to the fact that they must have spread from a common centre.

In the case of *Scaeops grandisquama* the above hypothetical mode of dispersal would fall under the second heading. There appear to be very many factors against such a method of spreading, so that the first condition, viz. multiple origin, may be looked upon as a more ready way of obviating the difficulty. An explanation of the other examples of Discontinuous Distribution and Cosmopolitan Distribution would also be afforded by these statements.

18. *Pseudorhombus russelli* (Gray).

It has been found in Durban Harbour, and also on the Natal coast within five miles of the mouth of the Umbilo River. It was recently recorded from Delagoa Bay.

It has been recorded from the east coast of India, the Bay of Bengal, Andaman Islands, Java Sea, coast of China, East Indies, and coast of New South Wales.

This species has probably the widest range of all the Heterosomata occurring in South Africa. It was recorded from the Inner Harbour, Durban, as *P. andersoni*, Gilchrist, but this specimen was subsequently found to be merely an abnormally developed form of *P. russelli*.

22A. *Pardachirus marmoratus* (Lacépède).

This species has been described from the Red Sea and Madagascar. It was recorded by Günther from the eastern coasts of Africa and by me (17) from Bazaruto (St. Carolina), shore-collecting amongst coral.

25. *Solea impar*, Bennett.

This species was recorded by Boulenger as *S. bleekeri* from the Cape of Good Hope. It has not since been recorded from South African waters, and it is doubtful whether the locality recorded was correct. It has also been described from the north-west coast of Africa and the Mediterranean.

31. *Aesopia cornuta* (Day).

It has also been recorded from off Amatikulu, Conical Hill, N.W. 7½ miles, in 26 fms., and from Delagoa Bay.

It is fairly widely distributed in Oriental waters, having been described from the Coromandel coast of India and north to Nagasaki, Japan.

From this distribution it may be inferred that there must have been some connection between Japanese waters and the Indian Ocean, this connection being extendable to the east coast of Africa, as suggested in Part I.

46. *Cynoglossus lida*, Day.

This species has been recorded from Durban. It has also been described from the coasts of India, Burma, and the Malay Archipelago.

III. Discontinuous Distribution.

Under this division those species occurring in widely separated seas and only recorded from two localities are grouped. There are seven species which may be looked upon as showing a Discontinuous Distribution, and of these four are recorded from the Pacific and from Natal, two from the Atlantic and from Natal, and one is recorded from the south coast and from north-west of Africa.

1. *Platophrys pantherinus* (Günther).

This species has only been recorded from Natal and from the Fiji Islands.

10. *Etropus* sp., von Bonde.

This species has already been described under the species endemic to the Natal coast, but the species with whose larval form it closely agrees was recorded as *Etropus remosus*, Goode and Bean, from the Gulf of Mexico. Until the exact species has been determined it will be impossible definitely to fix the distribution of the present species. It was an immature specimen, provisionally named as above, from the deep water of the Natal coast.

11. *Lambdopsetta kitaharae*, Smith and Pope.

This species was originally recorded from Kugoshima, Japan, in 1907. In 1920 it was found by the S.S. *Pickle* off the Natal coast.

21. *Limanda beanii*, Goode and Bean.

It has been recorded by Goode and Bean (1881) from the Atlantic Basin, 39° 57′ N. lat., and 70° 57′ 30″ W. long., 126 fms.; and 39° 57′ lat. and 70° 56′ W. long., 120 fms. Also off St Kitt's in 208 fms. and 250 fms.

The South African localities are all on the east coast.

In connection with this distribution it may be well to recall the fact that the Agulhas current has an indirect connection with the Gulf of Mexico, as explained in Part I under the heading Currents.

36. *Synaptura punctatissima*, Peters.

This species has been recorded by Steindachner from Algoa Bay, and by Peters from Victoria, West Africa. It is of rare occurrence, as it has not been recorded again from these or other localities.

39. *Plagusia marmorata*, var. *africana*, Gilchrist.

This variety was recorded from the Natal coast.

The original species, *P. marmorata*, Bleeker, was recorded from the East Indies.

The variety *africana* has already been recorded as an endemic species, but it is interesting to note the occurrence of a closely related species in the East Indies.

52. *Symphurus strictus*, Gilbert.

This species was recorded by Gilbert from off the coast of Oahu Island, Hawaiian Archipelago, depth 265–280 fms. An interesting parallel case is seen in the distribution of *Malthopsis stellatus*, Gilbert (fam. Malthidae), and an Alcyonarian, *Verrucella bicolor*, Nutting, both occurring at the Hawaiian Islands and off the Natal coast.

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A STUDY OF THE FRESHWATER ISOPODAN AND AMPHIPODAN CRUSTACEA OF SOUTH AFRICA.

By K. H. Barnard, D.Sc., F.L.S., F.R.S.S.Afr.

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(With Plates V–XI and nine Text-figures.)

CONTENTS.

Introduction.

This paper contains an account of some researches into the biology of the freshwater Isopod and Amphipod Crustaceans of South Africa.

These researches,* begun many years ago, are still being continued; but it seems that the results so far obtained should be published in the hope of inducing other naturalists to take up and extend the study. These animals are chiefly abundant in the mountainous districts of the S.W. Cape,

* Part of these researches was carried out by the aid of a Research Grant (1917), for which I am under obligations to the Council of the Royal Society of South Africa.

where they form a characteristic component of the fauna. The fauna in this region is a disappearing one, due largely to the practice of veld-burning, and no time should be lost in carrying out a thorough survey.

One of the main points in these biological investigations has been the study of the habitats of the animals in relation to the local topography and geology. This has led to results which, in addition to their intrinsic interest, may prove of value in a wider discussion on the origin of this fauna.

This method is especially valuable in the case of the particular groups of Crustacea here studied, because they alone among the Crustacea are dependent for their distribution and dispersal on the continuity of the river systems. Crabs can migrate overland from one river system to another; the *Entomostraca* lay resting eggs which can be dispersed far and wide by wind and other agencies. But the history of the Isopods and Amphipods is inextricably bound up with the history of the river systems and denudation of the country.

I am under obligations to several friends. Dr. Chilton of Christchurch, New Zealand, very kindly sent me specimens of *Phreatoicus australis* from Mount Kosciusko and *P. kirki*, var. *dunedinensis* from New Zealand, which specimens have been extremely useful for comparison with the Cape species. In describing certain points in the anatomy of these Australasian species I have but indicated the wide field for research in this group of animals that lies in front of the naturalists of those countries.

I have also to thank many mountaineering friends who have interested themselves in helping me to collect specimens, and especially my friend and colleague Dr. S. H. Haughton, whose kindly interest and criticism have helped towards a clearer presentment of the argument.

Historical.

The history of the South African freshwater Edriophthalmous Crustacea is a short one, dating back not much more than a decade, barring a few earlier records without adequate details.

Up to the present only one freshwater Isopod has been recorded. According to the published records *Phreatoicus capensis* Brnrd. was first discovered on Table Mountain in 1913 by Mr. C. French of Cape Town, an amateur naturalist who has contributed many interesting specimens to the South African Museum collections. Although mention was made of a prior claim no specimens in support of such claim were at the time, or have been since, produced. It is scarcely conceivable that the author of this claim would have refrained from collecting specimens of such an important animal, or from announcing the discovery; I maintain, therefore, that the credit of the discovery is due to Mr. French.

The discovery was announced in Nature, 1913 (**3**, p. 372) and the species was described and figured in 1914 (**4**, p. 233).

This single species of *Phreatoicus* and a member of another family, to be described below, are the sole freshwater representatives of the *Isopoda* in this country as yet known.

The Amphipods are more abundant. In 1843, Krauss (**20**, p. 60) recorded the European *Gammarus pulex* from Zoetendals Valley, Swellendam District. He found the specimens in brackish water, and for this reason Stebbing (Gen. Cat. S. A. Crust., 1910, p. 456) has thrown doubt on the identification.

Since Krauss' time no other record of *Gammarus* or any freshwater Amphipods has appeared until 1916, with the exception of Max Weber's record of an Amphipod from somewhere in Cape Colony (**43**, p. 186) and a bare record of a species of *Gammarus* being found associated with some aquatic worms on Stellenbosch Mountains (Goddard, 1913, Tr. Roy. Soc., S. A., iii, 2, p. 232). Although recorded in a paper on the freshwater fauna of South Africa, Max Weber does not actually state that his Amphipods were aquatic. I am rather inclined to think that they may have been the ubiquitous *terrestrial* Talitrid *Talitriator africanus* (Bate).

The presence of *Gammarus* was, however, known to the late Dr. W. F. Purcell, who collected several specimens while he was on the staff of the South African Museum.

On my arrival in South Africa, and then unaware of Dr. Purcell's collecting, I found these animals in the streams on Table Mountain. Since then I have systematically searched such mountain and other localities as I have had opportunities of visiting. Four species from Table Mountain were described in 1916 (**5**, p. 202).

In 1911, Methuen (**23, 24**) described an interesting blind Gammarid from the Makapan Caves in the Transvaal. It has been provisionally assigned to the genus *Eucrangonyx* to which it seems to approximate most closely.

Thus only one Isopod and five Amphipods have been recorded to date. In this paper another Isopod and six more Gammarids will be described, making a total of thirteen.

I. Phreatoicus Capensis.

A. *Anatomy*.

Only two very brief accounts have been given of the internal anatomy of the *Phreatoicidae*. Chilton (**12**) described the testes. Smith (**33**) in a few lines gave a very superficial account of the digestive organs, and

several of his statements, in view of their conflict with my results, must remain very doubtful until confirmed.

I have therefore endeavoured to elucidate certain points a little more fully by means of dissections and serial sections.

Legs and Gait.—The legs of *Phreatoicus* are divided into an anterior series of 4 and a posterior series of 3, as in many other Isopods (e.g. *Stenetrium*, *Munnopsis*, *Tanais*) and in Amphipods.

Phreatoicus "walks" like an Amphipod (Tait, **39**), but the limb-taxis is really more Isopodan than Amphipodan, owing to the absence of side-plates which confine the Amphipodan limbs to a fore and aft movement.

The basipodites of the four front limbs have a distinct latero-median trend; true, not as strongly marked as in a broadly depressed form such as *Ligia*, but yet not so distinctly Amphipodan as the illustrations lead one to expect.

When crawling the legs are seen in dorsal view to be splayed all around the animal. The 5th can be moved forwards a little in advance of a line perpendicular to the long axis and moves backwards through an angle of 90°. The 6th and 7th limbs have a proportionately less angle of movement.

All the limbs can on occasion, such as crawling through weeds, be elevated over the back, even the gnathopods rising above the top of the head.

The uropods are used, though not continuously, to help push the animal along—the movement is a slow steady push, not the convulsive "kick" of an Amphipod. The animals neither swim on their backs nor propel themselves along on their sides, but always (on a flat surface) walk erect. When dropped into the water they always sink passively to the bottom, though on one occasion I have seen them wriggle—the whole body bending backwards and forwards somewhat like a worm, but not with convulsive flexing and straightening of the pleon as in Amphipods.

A curious point is the modification of the 4th peraeopod in the ♂ (Barnard, **4**, pl. xxiv) corresponding with a similar modification of the same leg in certain species of *Asellus*, e.g. *A. communis* (Racovitza, **26**).

This may be looked upon as farther evidence that the *Phreatoicidae* are closely allied to the *Asellidae*, and that the two families have diverged from a common stock (*cf.* Chilton, **12**, pp. 208, 209).

Stomach (*Fore-gut*) (Pl. V.).—Smith (**33**, pl. xii. fig. 13) has given a figure of the gastric mill of *Phreatoicopsis terricola*. The figure shows two antero-lateral triturating surfaces, each followed by two narrow spinose ridges. On the floor of the stomach there appear to be two nearly contiguous triturating plates followed by a posteriorly widening surface armed with several transverse rows of setae. As there is no accompanying description the actual form and relationships of these plates and ridges is

somewhat obscure, and a re-examination of the stomach of this species would be most welcome.

The structure of the gastric mill in *P. capensis* allows little or no comparison with Smith's figures. On the contrary it is strictly comparable with that of *Asellus*, *Ligia*, and other typical Isopods (Barnard, **8,** p. 31).

At the anterior end there are the usual two dorso-lateral triturating pads armed with short spinules. Between these is a small medio-dorsal tooth, set with spinules and projecting freely backwards. When the stomach is compressed this backward projection is embraced by the two lateral pads, for which purpose there is a shallow groove in each running obliquely backwards. (Pl. IX, figs. 1, 2.)

Ventrally there is a small medio-ventral tooth or ridge lying at the bottom of a shallow groove, the sides of which are raised up into two parallel longitudinal striated keels. The edge of each of these keels is set with a regular close-set row of long spinules like a comb. (Pl. IX, figs. 1, 2.)

Passing backwards these comb-bearing keels (ventral striated ridges) peter out almost completely, but reappear farther back as the two ventro-lateral ridges which rapidly increase in size. They form the borders of a groove from the floor of which arises the medio-ventral posterior tooth. This groove deepens rapidly, and at the same time the bordering ridges and the median tooth become higher. The latter, however, never reaches as high as the former. Its upper edge is tricarinate. The upper edges of the ventro-lateral ridges are setose. The relations of these structures are made clearer by means of the figures. (Pl. IX, figs. 1, 4–6.)

The ventro-lateral ridges decrease in height quickly at the posterior boundary of the stomach, becoming almost obsolete. They are, however, continued into the intestine as will be described below. Before they become obsolete, the medio-ventral tooth ceases to be attached to the floor of the groove and becomes a freely projecting tooth, triangular in section and apically setose.

Immediately previous to the medio-ventral tooth becoming free, the ducts of the hepato-pancreatic glands open on either side of it into the ventral groove. (Pl. IX, fig. 6.)

A row of setae runs obliquely along each side of the stomach from the anterior triturating pad to the lower surface near the posterior margin of the stomach, where two thin lamellae arise (the ventro-lateral lamellae) which project freely into the intestine and are apically rounded and setose. (Pl. IX, fig. 1.)

The dorsal lamina, so conspicuous in *Asellus*, is here represented only by a slight transverse ridge which is sparsely setose.

Nearly the whole of the interior surface of the dorsal and ventral walls of the stomach is minutely setulose.

In *P. kirki* var. *dunedinensis* the stomach appears to have essentially the same structure.

An important external feature of the stomach is the muscle attachment to the posterior medio-ventral tooth. This muscle is single for a short distance, and then bifurcates into two long slender tendons attached to the sternite posterior to the lower lip (Barnard, **8,** text-fig. 1a). (Pl. IX, fig. 1.)

Intestine (Mid- and Hind-gut).—Smith (**33,** p. 71, pl. xii, figs. 12, 13) describes and figures a "typhlosole" in the intestine of *Phreatoicopsis terricola.* It arises in the median ventral line and then divides into right and left lamellae, which are longitudinally coiled upon themselves, each appearing in section like a ram's horn. Smith states that he has found a similar typhlosole "in the various species of *Phreatoicus,*" but does not state the particular species.

Such a typhlosole, as the author remarks, is quite unique among the Crustacea. The so-called typhlosole in *Ligia*, mentioned by Hewitt (**18,** p. 16, pl. ii, fig. 16), is, I believe, merely an accidental invagination due to the mode of preservation or distortion in the process of section-cutting (see also *infra*), as I have not found any such invagination either in *Ligia oceanica* or the Cape species.

So far, however, from this typhlosole being a characteristic of the whole family of *Phreatoicidae*, it is here shown to be absent in the Cape species, the Australian *P. australis*, and the New Zealand *P. kirki* var. *dunedinensis.*

Smith does not specify which species of *Phreatoicus* he examined, but as he was dealing mainly with Tasmanian material, it may be assumed that he examined *P. australis* which occurs on Mount Wellington. Specimens of this species from this locality were examined in the course of the present investigation and likewise found to lend no support to Smith's statements.

In the Cape species the intestine from beginning to end is a perfectly simple tube, as is normal in the majority of Isopods. A rectal portion (hind-gut) is not distinguishable from the mid-gut.

At the extreme anterior end there is a ventral groove which may serve both to store and to convey to the food-mass the secretion of the hepatio-pancreatic glands. The ventral groove, with its bordering (ventro-lateral) ridges, which contains the medio-ventral tooth at the posterior margin of the stomach, is continued into the intestine. At first it is very shallow, and the ridges can be traced only by the closer aggregation of the cell nuclei on the wall of the intestine. Farther back these cells become elongate and form a distinct groove. The ridges then approximate, enclosing a deep groove, and eventually fuse. The groove is continued backwards for a short distance as a blind pocket, posterior to which the intestine

assumes, in section, a simple oval or subcircular shape. (Pl. IX, figs. 1, 9–12.)

The cells lining the ventral groove and pocket are regular and quadrate, with moderate-sized nuclei, quite distinct from those lining the dorsal and lateral portions. These latter cells are large, oblong, somewhat irregular, with very large nuclei, and are arranged in definite rows running obliquely backwards and downwards from the median dorsal line. This arrangement continues back to the rectum. (Pl. IX, figs. 9–12.)

In the specimen of *P. kirki*, var. *dunedinensis*, which was examined by means of serial sections, the intestine in transverse section resembled very much the figure given by Hewitt (**18,** pl. ii) of the intestine of *Ligia*. There is a slight dorsal longitudinal ridge, the so-called typhlosole (Hewitt, pl. ii, fig. 16), and the floor is raised up in a **Λ**-shape. This may be due to the specimen being in the act of ecdysis or to the method of preservation. In two other specimens, the anterior portion (1st peraeon segment) of the intestine showed the ventral invagination, but farther back the internal organs were not well enough preserved to show any definite features.

I am inclined to think, therefore, that Smith must have examined specimens which were in process of moulting, and that this accounts for his thinking he had discovered a "typhlosole."

Hepato-Pancreatic Glands (Pl. IX).—Smith (**33,** p. 72) gives the number of glands in *Phreatoicopsis terricola* as 4.

In *P. capensis* there are 3 pairs of glands extending back well into the pleon, remaining separate throughout their entire length. Anteriorly the lateral gland may pass into the ventro-lateral and then both pass into the ventral, or the ventro-lateral may pass into the ventral before the lateral gland joins up. The united glands pass into the ventral groove of the stomach at the spot where the medio-ventral tooth becomes free. This corresponds about with the base of the maxillipeds. (Pl. IX, figs. 1, 6, 9–12.)

There is a single tubular forward extension of the hepatic glands on either side, similar to that found in *Ligia* (Hewitt, **18,** p. 17).

These extensions reach to about the anterior end of the stomach and histologically are similar to the posterior portions, being composed of a single layer of large nucleated cells surrounding a central lumen.

In *P. australis* and *P. kirki*, var. *dunedinensis*, there are also 6 glands uniting into a single duct opening at the same position as in *capensis* and possessing also the forward extensions.

Salivary Glands.—No trace of any glands opening into the oesophagus was found.

Maxillary Glands.—Smith (**33,** p. 72) mentions the very large maxillary

glands. *P. capensis* and *kirki*, var. *dunedinensis*, are in accordance with this statement.

The two glands lie below the anterior portion of the stomach, almost meeting in the middle line, and opening on the inside of the bases of the 2nd maxillae.

In section they are seen to be composed of a number of irregularly oval or rounded cavities with occasional very large cell nuclei on or in the dividing walls.

Nervous System.—This consists of the supra- and sub-oesophageal ganglia and a ventral chain of 7 thoracic and 6 abdominal ganglia.

The supra-oesophageal ganglion consists of two simple lobes, with very shallow dividing groove.

An optic ganglion is absent.

The two interganglionic thoracic and abdominal cords are distinct, but not widely separated. As would be expected there is a ganglion to each abdominal segment, including the last or telsonic segment. The telsonic ganglion, however, is not situate in its proper segment, but has been shifted forwards into the 5th segment, being immediately behind, though not quite contiguous with, the 5th abdominal ganglion. Posteriorly the 6th ganglion gives off two slightly diverging, moderately stout nerves to the telson and uropods.

I have not specially endeavoured to obtain sections of the eyes. Those obtained incidentally in the course of cutting sections of the head show that a certain amount of degeneration has set in, though not to any great extent. Retinal pigment is still developed.

Male Reproductive Organs.—Chilton (**12,** p. 196) examined the testes and spermatozoa in *Phreatoicus assimilis* and stated that in general they resembled those of *Asellus aquaticus*, but possessed a greater number, 5–6, of oval testes. He found also that the spermatozoa resembled those of *A. aquaticus*.

In *P. capensis* the number of testes is still greater, varying from 8–10 on each side. Sometimes the numbers on the two sides do not correspond. As in *Asellus* they are oval, without thread-like processes. They extend forwards as far as about the junction between the 2nd and 3rd peraeon segments.

The vasa deferentia are covered with black pigment, some of which also is often visible in the interior of the external styliform appendages or penes; they are of equal width throughout, only narrowing when they bend downwards to pass into the penes.

The spermatozoa are similar to those of *Asellus aquaticus*.

Female Reproductive Organs.—These are perfectly normal, showing no special peculiarities.

The brood-pouch was originally described as being composed of 3 pairs of lamellae arising from the bases of the 2nd–4th pairs of peraeopods. All mention of the lamellae on the 1st segment was, however, omitted. In the possession of 4 pairs, *Phreatoicus* thus resembles *Asellus*.

All 4 pairs have a somewhat opaque central part surrounded by a transparent border. The posterior borders of the 4th pair have a number of rather widely spaced simple setae.

The 1st pair are similar to the 1st pair in *Asellus* in being bent in the middle so as to form a larger posterior lobe and smaller anterior lobe. The posterior lobes resemble the other lamellae and form part of the brood-

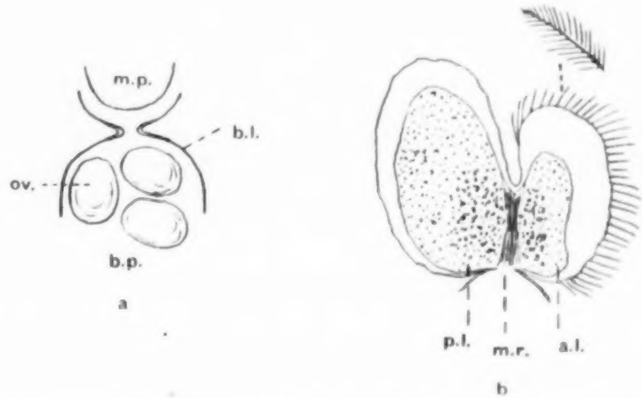


FIG. 1.—*Phreatoicus capensis.* a, Diagrammatic plan showing 1st brood lamella (*b.l.*), embracing mouth-parts (*m.p.*) and forming part of brood-pouch (*b.p.*) b, 1st brood lamella flattened out, showing midrib (*m.r.*) and anterior and posterior lobes (*a.l.*, *p.l.*).

pouch. The anterior lobes, however, embrace the projecting mass formed by the mouth-parts. The anterior margins of the anterior lobes are furnished with a row of close-set plumose setae, which allow the lobes to be closely applied to the epipods of the maxillipeds.

In addition to the anterior lobes being closely applied to the maxillipeds, it is possible for the brood-pouch to be still farther closed by the juxtaposition of what may be called the "midribs" of the lamellae (see fig. 1).

I do not know of any similar arrangement of the lamellae of the brood-pouch in other Isopods, and it is significant finding this arrangement in both *Phreatoicus* and *Asellus*.

The number of ova produced varies from about 7–15, but the number of embryos that reach maturity is usually less (5–12).

B. *Embryology.*

I do not intend to give a detailed account of the development, but merely to draw attention to the fact that it is typically Isopodan, and that the embryo bears a striking resemblance to that of *Asellus* in one particular feature.

The embryo has the dorsal curvature characteristic of the Isopoda, and possesses a pair of dorsal appendages similar to those found in *Asellus aquaticus*. (Pl. IX, fig. 13.)

These appendages differ in shape from those of *Asellus aquaticus*, being rounded instead of trilobed.

The function of these appendages still remains obscure. It has been suggested that they convey an albuminous fluid in the brood-pouch to the embryo. Sars (**28,** p. 121) discusses the question. He points out that other Isopods, e.g. *Jaera*, get on quite well without these structures.

The discovery that *Phreatoicus* resembles *Asellus* in this particular is of importance, as it points to the two genera having a common phylogenetic ancestry. On the other hand there is the alternative possibility that this structure has been independently developed in response to the freshwater environment.

In this connection the embryos of *Protojanira* (see *infra* p. 163) were examined, but it was found that no such appendages are developed in this genus, which is also freshwater.

I am not aware whether this structure has been observed in the other species of the genus *Asellus*. The other species of the *Phreatoicidae* should also be examined, though there is little doubt that the possession of these appendages will prove to be a family characteristic.

C. *Biology.*

Habitat and General Habits.—The localities where *Phreatoicus* has been found are:

(1) On the top of Table Mountain in the Cape Peninsula.
(2) In the Hottentots Holland Mountains, from Landrost Kop (near the Sneeuwkop) southwards to the Steenbras Valley and the Kogelberg.
(3) In the Zonder End Mountains.
(4) In the Langebergen in the neighbourhood of Swellendam and the Tradouw Pass, and Riversdale.

The habitat is much the same in all the localities. In the original description it was stated that on Table Mountain the animals were found in a ". . . swiftly running stream." This is rather misleading. I have

since determined that the spot referred to is the *lowest* spot in that stream where the animals can be found. At this point the stream is just passing out of the broad valley, through which it slowly meanders, to enter a more tumultuous course over a rocky bed. The animals are moderately abundant here, living in the moss (*Chiloscyphus* *) which covers the stones on the bed of the stream and along the banks.

But they are far more abundant in the upper reaches where the meandering stream is cut up into a series of more or less disconnected pools, continuous only in the winter time and stagnant in summer. The bottom of the stream and especially of the pools is a thick deposit of humid mud. (Pl. VI, figs. 1, 2; Pl. VIII, fig. 2.)

The vegetation of these pools consists of an abundant growth of moss (*Sphagnum* and *Dicranum*), and a species of *Scirpus* (*S. fluitans* var.).

The animals live among the bases of these plants and in the upper layer of mud. They seem to spend all their time there, though occasionally I have seen them crawling along the stems of the *Scirpus* towards the surface of the water. The few occasions on which I have observed this have always been on hot, sunny days.

During the night they are somewhat more active and venturesome, especially when kept in captivity.

In the other localities the animals inhabit similar situations: pools in the courses of slowly running meandering streams, and the moss- and debris-choked runnels flowing into these.

In the Steenbras Valley quite small runnels, often only a few inches wide, are thickly populated with *Phreatoicus* during the wet season, evidently finding their way there from other more permanent runnels, or tiding over the dry season by aestivating in holes as described below. In this locality also the animals thrive in marshy spots where the water must be stagnant all the year round.

The important point to notice is that the animals are confined to those portions of the stream where the current is not too strong to prevent the growth of moss and the accumulation of humid mud. It is quite useless to search typical "mountain streams" where the water tumbles over boulders and scours out its bed. Contrast Pl. VI, fig. 2 with Pl. VII, fig. 2.

When handled or otherwise disturbed, the animals curl up and remain quiet for a few minutes and then at once proceed to bury themselves in the mud or crawl out of sight amongst the vegetation. If dropped into the water they sink passively to the bottom, making no attempt to swim, and then proceed to bury themselves.

An exception to this was noticed on one occasion in the Hottentots

* I have to thank Dr. T. R. Sim of Pietermaritzburg for the identification of several samples of moss.

Holland. The animals seemed to be in a very irritable condition. Whenever touched either when crawling along the bottom or when dropped into the water, the body was violently jerked from side to side, in the same way as a caterpillar resents being touched when it is just about to change into a chrysalis. A similar state of irritability can be produced artificially by gently warming a vessel of water containing some of the animals, and I conclude, therefore, that the irritability of the animals observed in the field was due to the unpleasantly high temperature of the water on that occasion.

Rate of Growth.—By assiduous collecting throughout a number of years, certain data on this point have been obtained. The results, however,

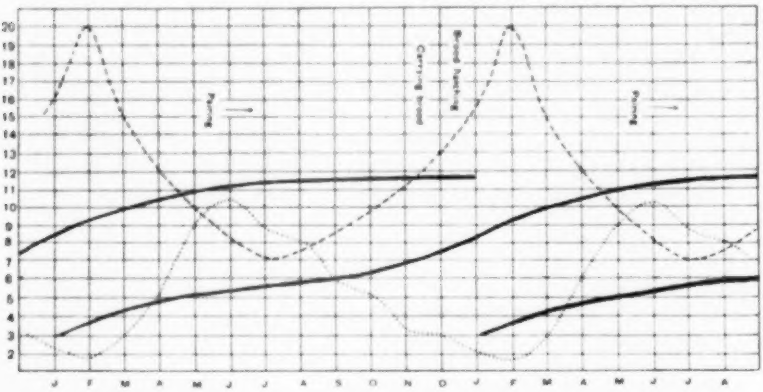


Fig. 2.—Chart to show rate of growth of *Phreatoicus capensis* on Table Mt. (heavy line). Ordinates: months of the year. Abscissae: length of animals in millimetres; temperature of water (broken line) in degrees centigrade; rainfall (dotted line) in inches.

should not be regarded as absolutely final, since still further observations might perhaps alter them. Nor can they be checked or supported by observations on animals in captivity.

Further, the results apply only to the colonies living on Table Mountain, as the other localities have not been visited frequently enough. Temperature records were also taken, and the resultant curve represents the averages for several years.

In plotting the results the measurements were found to aggregate into definite bands, and by drawing lines through the densest parts of these bands the average growth-curves represented in the accompanying diagram were obtained (text-fig. 2).

Some few exceptional cases were encountered, which could not be included in the limits of either band. Such examples were only to be ex-

pected, since sickly or diseased individuals would probably be stunted in growth and thus be below the normal. Others again, owing to unusually favourable circumstances, might be exceptionally large for their age.

The young start their independent existence at the end of December and beginning of January. They are then about 3 mm. in length. The rate of growth gradually increases until about May, when it becomes somewhat slower, coinciding with the winter season and the low temperature of the water. After July the rate increases again, and continues through the summer until the following May, when the animals are full-grown.

They are thus biennial, although it is just possible that some of them start breeding in the first summer after their birth. But from considerations of size I do not think so, although I have no actual proof one way or the other. The point might be solved if the animals could be kept under observation in the laboratory. If they breed in the first summer, the farther question arises whether they survive to the following summer and produce a second brood. This is improbable in the ♀♀ at any rate, for reasons stated below (p. 152).

Owing to inability to keep the animals longer than a month or two under laboratory conditions, I am unable to state the number of exuviations through which they pass.

Mating and Period of Breeding.—From the beginning of May onwards pairing takes place. Mated pairs are everywhere to be found at this season; in fact, single specimens other than young immature ones are so rare that a very close equality in the number of individuals of each sex may be inferred (text-fig. 2).

Pairing continues up to November, when the females are found with ova in the brood pouches. The question, therefore, arises whether the same male carries the same female for upwards of six months. It seems highly improbable that such fidelity does occur, but it is difficult to adduce decisive evidence owing to the failure of attempts to keep the animals under observation in the laboratory.

Several pairs have been isolated in dishes and have survived for so long as a month, during which time the male was never observed to leave hold of the female, but the experiment is inconclusive for several obvious reasons. For the same period also several pairs have been kept in one dish, each male and female being marked by having the tip of one antenna or joint of a particular leg removed. No change of partners was observed. Beyond a month under laboratory conditions the animals do not seem able to survive.

Sars (**28**, p. 116) notes that the ♂ carries the ♀ for many days, and Unwin (**41**) has drawn attention to the marriage-clasp and its significance in *Asellus aquaticus*. The ♂ clasps the ♀ until she casts the cuticle from the

posterior half of the body (5th peraeon segment backwards), when copulation takes place. After this he releases her, the cuticle from the front half of the body is cast, the brood-plates are formed, and the eggs pass out into the brood pouch.

In November and December, after copulation and the extrusion of the broods into the pouches, there seems to be a marked numerical preponderance of females, as if the mortality among the males was rather great at this period. They do not, however, all die, because a month later, when the broods have been hatched, the preponderance is reversed in favour of the males.

In fact on one occasion when collecting in the Hottentots Holland Mountains numbers of males and newly hatched young were found and not a single female.

So that apparently the females die after the hatching of the brood. In captivity they certainly do, sometimes just before, sometimes shortly after, the young have escaped from the pouch. This procedure is not without parallel among Isopods, for although I know of no record of the fact in the literature, several cases among the *Sphaeromidae* have come under my own observation.*

In case, however, they do not die after producing one brood, do the females breed a second time? From considerations of size (see growth-curve, fig. 2) any possibility of this seems excluded in the case of *Phreatoicus*, though it should be noted that the females of *Asellus* certainly breed more than once.

The escape of the young from the brood pouch takes place at the end of December and beginning of January on Table Mountain, or perhaps a little earlier in the Hottentots Holland Mountains.

It is important to notice the time of year at which the broods are produced. As a general rule, where the seasons are well differentiated, the young of any animal are produced at the season most favourable to their further growth, although perhaps if a wide survey were taken many divergences would be found. Such divergencies might afford valuable corroborative evidence of past changes either in the habits of the animal or in the climatic environment.

In the case of *Phreatoicus*, as stated above, the brood is produced in late December or early January, i.e. in early or mid summer. This means

* At Plymouth I have observed the females of *Naesa bidentata* to die after the escape of the brood, and in this country I have seen the same happen in the case of *Parisocladus Stimpsoni* (Hell.).

It should be noted that in the case of *Naesa* death could hardly be avoided, because the brood being contained in pouches *within* the body, the internal organs are more or less atrophied. After the escape of the brood there is merely the empty shell of the female left.

that the wettest and coldest months are past (pairing took place during this season), but that the water temperature has not yet reached its maximum, nor has the late summer drought set in. In this respect it is quite on a par with *Asellus* in the Northern Hemisphere.

Now if we assume that a drought is an adverse condition which might affect the newly born animals more seriously than half-grown or older animals, having thus the same effect as cold and frost in higher latitudes, then we see that *Phreatoicus* completes its breeding only just in time. On Table Mountain the streams are liable to run dry in late February or early March, or in the Hottentots Holland earlier still, forcing the animals to aestivate in the damp mud. In the latter locality the time of liberating the brood from the maternal pouch seems to be earlier, and thus apparently an adaptation in conformity with the climate.

If this latter observation be correct we wonder whether *Phreatoicus* was not once accustomed to a colder and moister climate, a climate at least in which there was no danger of a drought. We have, however, no collateral evidence from the other species, and thus are merely entering the realms of speculation.

But why the long period of mating, extending over six months? I find no satisfactory explanation of this fact. Note that the water temperature is the same at the beginning (May) as it is immediately before the females appear with brood (November). Does this show that there is a certain optimum temperature for exuviation and producing a brood, and that the pairing in May is an attempt to breed, which is cut short by the advent of colder weather? Or does it show a greater persistency in the females of an age-long rhythm in response to which the production of a brood coincides with the spring rise in temperature after the winter's cold?

Food.—The food consists of the vegetable mud which is found at the bottom of the streams and pools and at the bases of the moss and water-weeds in which the animals live. A few larger vegetable fragments, such as portion sof Sphagnum moss, are found mixed in with the other food, their presence being probably merely accidental.

In a few cases, however, the whole alimentary canal was found to be filled with fragments of Sphagnum, so fresh looking that they must have been bitten off the green growing shoots of the moss.

Phreatoicus does not seem to be attracted by fruit or animal matter, and cannot be decoyed into a net baited with these substances as can *Gammarus nigroculus*. In the Zonder End Mountains, however, I have collected *Phreatoicus* in enormous numbers by leaving a saucepan, in which porridge had been cooked, unwashed in the stream overnight.

Enemies.—No actual encounters have been witnessed, but the following field experiments bear upon this subject.

On Table Mountain and in the Hottentots Holland Mountains specimens of the crustacean were dropped and placed near frogs (*Rana fuscigula*) and were greedily snapped up both in the water and on the bank at the water's edge. Moreover, since frogs will jump at almost anything, animate or inanimate, that drops into the water from the overhanging rushes on the bank, a spot was chosen free from water-weeds, and while all the frogs were temporarily scared and concealed at the bottom, some *Phreatoicus* were quietly placed in the water and allowed to scatter in all directions. When the frogs came out and began to ascend to the surface and the water's edge they caught sight of the *Phreatoicus*, and as before gobbled them up.

Thus, as far as possible, the natural conditions were reproduced showing that when the crustaceans wander from their protected haunts among the bases of the water-weeds they are liable to be immediately devoured.

No opportunity of experiments with fishes has yet presented itself. In the Steenbras stream, *Phreatoicus* occurred with *Galaxias*, but even the largest of these (60–70 mm.) would scarcely be able to swallow a *Phreatoicus*. Moreover, *Galaxias* seems to prefer those spots where, owing to rocks or other obstructions, there are tiny waterfalls or rapids, in preference to the more stagnant parts of the stream, and thus rarely comes in actual contact with *Phreatoicus*.

Parasites.—No parasites, external or internal, have been noticed up to the present.

The ova in the brood pouch, however, have on several occasions been found to be completely matted together with and destroyed by the mycelium of some fungus.

Aestivation.—We come now to a rather curious phenomenon, which, so far as I am aware, is without parallel among the Isopods. Certain marine forms, of course, are accustomed to living in rock crevices, etc., which are actually under water only at high tide. But *Phreatoicus* is able to exist without actual water for a period of several weeks, even three or four months, as I have determined by laboratory experiments.

The first occasion on which I observed the animals aestivating was in the Hottentots Holland Mountains in January 1916. During my stay there, several pools which I had noticed were well stocked with the animals dried up, and I was puzzled to know what had become of the inmates, until I found them embedded at the bottom of little pits in the peaty mud. The pits were from one to two inches deep and each pit contained only a single animal. (Pl. VII, fig. 1.)

The peat was saturated with water, but there was no free water in the holes occupied by the animals, which consequently were breathing only the damp air. This peaty mud retains moisture for a long period, thus

the necessary moist atmosphere is maintained in the burrows of the animals until the next rain.

The aestivating animals, even after some weeks in that condition, are not at all sluggish, but when dug up uncurl themselves at once and, if dropped into water, proceed to bury themselves. They are thus able both to commence aestivation at any time and to resume their ordinary activities directly the drought breaks.

This habit of curling up at the bottom of a burrow has evidently become an instinct, for in the unusually severe drought in 1917, the colony on Table Mountain was found to have "dug itself in," and this colony had not been exposed to such conditions for at least five years previously.

While aestivating in their burrows the posterior part of the peraeon and the pleon are closely curled up. The 6th segment and telson are bent down between the pleura of the 5th segment. The rami of the uropods are bent at right angles to their peduncles and brought together so as to close in on the ventral side the branchial chamber. The setae (simple) on the margins of the pleura, as well as the spines and setae on the uropods, all help to close the cavity. Anteriorly it is closed to a large extent by the 2nd joints of the 7th peraeopods being curved in towards one another.

Although a unique occurrence among the Isopoda, this habit of aestivating is not altogether unexpected in *Phreatoicus*, in view of the fact that one of the Australian members of the family has given up entirely an aquatic mode of life and taken to burrowing in damp earth (Spencer and Hall, **35**, and Raff, **27**).

Chilton (**15**, p. 24) refers to the possibility of *P. latipes* becoming "encased in dried-up mud, retaining the power of vitality, and resuming activity as soon as the water reappears," but his remarks are not based on any actual facts.

D. *Variation.*

A detailed examination of the forms from different localities, taking the Table Mountain form as typical, shows that variation occurs mainly in the shape of the telson and the number of spines it carries, the length of the 2nd antennae, the shape of the hand of the gnathopod (1st peraeopod), the degree of setosity along the sides of the body, and the colouration.

All the forms possess the characters which are regarded as specific, and as distinguishing *capensis* from its nearest relative *australis* (see p. 158). This close resemblance among the specimens from different localities is interesting as showing the strong conservatism in these animals, a fact that will stand out even more prominently when the relationships between *capensis* and *australis* are discussed (p. 158).

The two extreme degrees of variation in the shape of the telson are shown by the Table Mountain and the Kogelberg forms (fig. 3). The number of spines along the margin of the telson (including the apical spines) varies between 6–8 or 9; sometimes there is an additional pair of subapical smaller spinules on the dorsal surface.

The 2nd antenna is usually not much longer than half the length of the body; but in some places in the Hottentots Holland Mountains, there are colonies with the 2nd antenna distinctly more than half, usually three quarters, the body length.

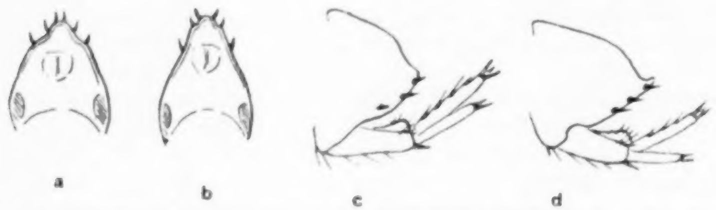


Fig. 3.—*Phreatoicus capensis.* Ventral and lateral views of telson of: a, c, Kogelberg form; b, d, typical form from Table Mountain.

In the shape of the hand of the gnathopod there is often considerable variation among the members of a single colony (fig. 5). The hand is, however, always more or less pyriform, except in the Kogelberg form, where a distinct varietal type seems to have become fixed (fig. 4).

Fig. 4.—*Phreatoicus capensis.* Outline of hand of gnathopod of: a, typical form from Table Mountain; b, Kogelberg form.

In one part of the Steenbras valley a very distinct variety occurs in which the body is considerably more depressed than normally, and the sides of the head and body are strongly setose (fig. 6).

In colouration the peraeopods and gnathopod, especially the 2nd joints of the former and the hand of the latter, are mottled with grey. The uropods and the flagella of the antennae are also grey in colour. Depigmentation or incipient albinism, however, occurs in some localities (e.g. some localities in the Hottentots Holland Mountains, and in the Swellendam Mountains) and all the appendages just mentioned are creamy-white, without any grey mottling.

Only two forms are considered worthy of varietal names, diagnosed as follows:

Var. *abbreviatus*, n. var.

Telson much more stumpy than in the typical form. Hand of gnathopod broad and ovate, with a straight hind margin and a well-defined angle

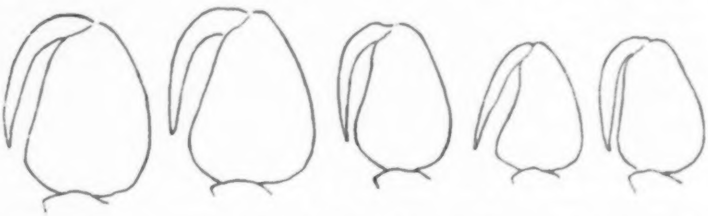
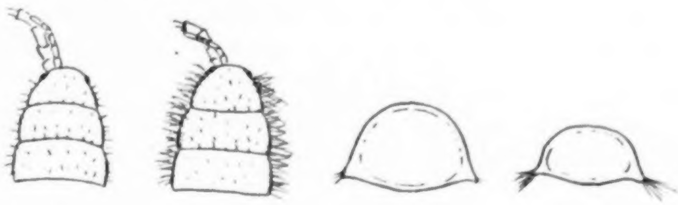


FIG. 5.—*Phreatoicus capensis.* Outlines of hand of gnathopod to show variation in shape in typical form from Table Mountain.

between it and the palm. Appendages pale in colour, with scarcely any grey mottling.

Locality.—Northern slopes of Kogelberg in the southern part of the Hottentots Holland Mountains.



a b c d

FIG. 6.—*Phreatoicus capensis.* Dorsal view of anterior part of body to show maximum amount of setosity in typical form from Table Mountain (a), and normal amount of setosity in Kogelberg form (b). c, d, transverse sections of body of Table Mountain and Kogelberg forms respectively.

Var. *depressus*, n. var.

Peraeon considerably more depressed than in other forms. Side-plates and lateral portions of head strongly setose. Telson not so stumpy as in the above variety, but more so than in the typical form. Hand of gnathopod pyriform. Colouration typical.

Locality.—Near the Forest Ranger's Hut in the Steenbras Valley, Hottentots Holland Mountains.

E. *Relation of* P. capensis *to the Other Members of the Family.*

Firstly a slight correction of my original description and discussion of the affinities is necessary. I exaggerated the length of the pleon, making the fraction $\frac{75}{100}$ instead of $\frac{60}{100}-\frac{70}{100}$. Thus *P. capensis* comes very much nearer to *P. australis*.

At that time also I had not seen any specimens of the typical *P. australis*, but later I received some of the original specimens from Mount Kosciusko, through Dr. Chilton's kindness. These specimens, though somewhat faded after many years in spirit, still show the pattern on the body and the bases of the peraeopods quite distinctly. This colour-pattern was referred to by Chilton (**11**, p. 152), but was not indicated in his figure. Therefore I did not realise how exactly similar, even in detail, this pattern was in *P. australis* and *capensis*. It is so remarkable that it deserves special attention, and is a most important character in discussing the affinities of the various species of Phreatoicids.

In general the colouration is a dark slaty grey, in many cases almost black, with lighter lateral mottlings, these mottlings taking more or less the form of a crescent on each of the peraeon and first 5 pleon segments.

The antennae, peraeopods and uropods partake of the same dark tint, though the peraeopods are lighter distally.

The following details are to be noted. On the head the light mottling is more abundant laterally where the light specks are more or less grouped together in series of 3 or 4, across the dorsal surface the specks run in somewhat irregular and interdigitating bands. The dorsal parts of the peraeon and pleon are almost uniformly dark. This broad medio-dorsal band is bordered laterally by the light crescentic markings on each peraeon and the 1st 5 pleon segments; below these marks the peraeon segments are mottled, the areas of dark and light being about equal. The pleura of the pleon segments are lighter along the *anterior* margins. The 5th pleon segment has 2 sub-dorsal small light spots.

The 2nd joint of all the peraeopods is dark with a fairly regular longitudinal row of light spots down the middle of the outer surface. The hand of the 1st peraeopod is mottled with rather large light spots, its distal end being dark, fingers also dark.

On the other hand, *P. capensis* is clearly distinguished from *australis* in the following characters: in the Cape species the eyes are much more prominent and bulging, the peduncle of the uropod has the inner upper margin much higher than the outer margin and has no large stout spines on its lower apex, and the rami are apically blunt and carry 2 spines.

In *australis* the eyes are nearly flat and not projecting beyond the plane of the cheeks, the peduncle of the uropod has both upper margins

equally high and neither of them as high as the inner one in *capensis*, there are 2 large stout spines on lower apex, and the rami taper distally and carry only 1 spine.

P. typicus and *assimilis* agree with *australis* in having the rami of the uropods each tipped with only one spine.

This close relationship between *capensis* and *australis*, as shown chiefly in the colour-pattern, is valuable as helping to decide whether the Australian or the Tasmanian form of *australis* is the older. This is the only Phreatoicid recorded from two now discontinuous land-masses, and the two forms cannot be structurally separated. There is, however, a distinct difference in size and in colour: the Tasmanian form being smaller and uniformly black.

Before the discovery of the Cape species there was really no evidence to enable one to decide whether the Tasmanian *australis* was derived from the Australian or vice versa. But the exact concordance in colour-pattern of *capensis* and *australis* leads one now to think that the Tasmanian form is the derivative. Perhaps its present variability according to locality is also an indication that it has not yet reached perfect stability; though this must not be too much insisted upon, because the same may also be said of *P. capensis*. Similarly the Australian form of *P. australis* may prove to be variable when further specimens are obtained from other localities near Mount Kosciusko.

F. *Evolutionary Tendencies within the Family.*

In discussing this topic the following salient features have to be taken into account:

1. The presence or absence of eyes.
2. The relation of length of pleon to that of rest of body.
3. The development of the pleural lamellae.
4. The epipods on the pleopods.

It is assumed that *P. capensis* and *australis*, being structurally the nearest together and geographically the widest apart, are the most primitive, or perhaps more correctly expressed, represent the ancestral stock.

Firstly, it is obvious that the ancestral stock must have been an eyed form. The blind species are later products.

In this connection it is interesting to observe how in *P. shephardi* the body pigment is more stable than the function of vision, whereas in *brevicaudatus* the reverse is true.

Secondly, the relationship of the pleon to the rest of the body is difficult to estimate accurately, as pointed out by Chilton (Tr. N. Z. Inst., xxxviii,

p. 275, 1906). It was wrongly estimated in my original description of *capensis* (see above), and Smith's figure of the Tasmanian *australis* seems likewise too high ($\frac{73}{100}$); at least none of the specimens I have examined from Mount Wellington exceeded $\frac{65}{100}$. But for our present purpose we do not need very great exactitude. The important point is that while the majority of forms possess a relatively long pleon amounting to about $\frac{60}{100}$–$\frac{80}{100}$ of the rest of the body, there are some which show an undoubted shortening of the pleon. Thus in *P. brevicaudatus* the fraction is $\frac{44}{100}$, in *Hypsimetopus* $\frac{48}{100}$, and in *Phreatoicoides* $\frac{36}{100}$.

P. brevicaudatus inhabits the "deeper littoral" according to Smith, which affords us little indication of the reason for this shortening. In the two other genera, however, we can plausibly account for it by the influence of the environment: *Hypsimetopus* being found in the burrows of *Engaeus* and probably itself burrowing, and *Phreatoicoides* has been definitely recorded by Sayce as burrowing among the fibres of rotting tree-fern trunks, in which habitat an elongate form is clearly advantageous. The low pleon-body fraction is here partly due, it is true, to the elongated peraeon, yet the pleon itself is undoubtedly reduced.

This reduction concerns the pleopod-bearing segments, and thus these species approximate to the more general present-day type of Isopod.

P. kirki, var. *dunedinensis*, seems to be evolving in the same direction.

Definitely correlated with the reduction of the pleon is the reduction in the development of the pleural lamellae. It occurs in the same two semi-terrestrial genera above mentioned, and seems also to be taking place in *Phreatoicopsis terricola*, though here it is not so evident.

The latter terrestrial species is an eyed form and may therefore be regarded as having taken to burrowing on land at a comparatively recent period.

The adoption of a terrestrial or semi-terrestrial mode of life, of course, exposes these animals to a much greater range and variation in external conditions, compared with the more uniform conditions under which the purely aquatic forms live, and this presumably has called forth the modifications we are discussing.

Hypsimetopus has progressed further and may perhaps on that account be regarded as having branched off earlier from the parent stock. But it has not reached the stage seen in *Phreatoicoides*, which is perhaps the oldest of the burrowing forms, as it has the relatively shortest pleon, no pleural lamellae, and the epipods, characteristic of all the other members of the family, are absent.

Although this series may represent so many stages in evolution, it does not follow that the last mentioned was really the first in point of time to strike into a new mode of life leading to the specialisation we now see.

While this must be borne in mind, nevertheless we do appear to be dealing here with an evolutionary series.

On the views here expressed the phylogenetic history of the family may be thus graphically represented.

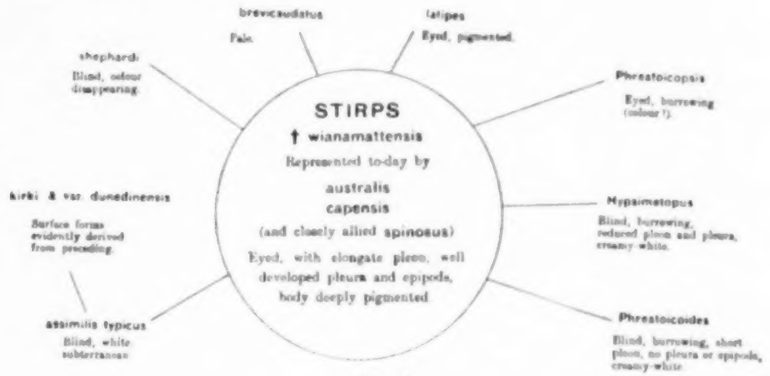


Fig. 7.

II. Other Isopoda.

Besides the *Phreatoicidae* there are but few Isopods of truly freshwater habitat, and with the possible exception of the *Asellidae*, they are scattered, and, no doubt, recent immigrants from the sea (Calman **10,** p. 279).

The freshwater representatives of the *Sphaeromidae*, *Idoteidae*, and other families, would certainly seem to bear out this latter statement; they are in no wise "conspicuously different in structure from marine representatives" (Calman, *ibid.*) of their respective families. The same may be assumed in the case of *Jaera guernei* Dollf. from the Azores.

The family *Jaeridae*, to which the last-mentioned form belongs, is a very large one and is represented in all depths of the ocean. In 1900, Sayce (**31,** p. 124) described a minute form belonging to this family from freshwater pools in Gippsland, Victoria, Australia.

This minute blind Jaerid (*Janirella* Sayce, later changed to *Heterias* Rich.) might also have been regarded as a comparatively recent descendant from marine ancestors. It possesses no particular features which distinguish it from the marine Jaerids.

The discovery, however, of a similar minute and blind Jaerid in South Africa may possibly be considered as indicating another explanation. The South African and Australian forms do not appear to be particularly closely allied, and the former has very distinctive features of its own, which distinguish it from all other Jaerids.

The presence of a freshwater genus of *Jaeridae* in Australia and another in South Africa, while freshwater representatives are apparently entirely absent from Europe and elsewhere, may not be without significance. Both genera are associated with the Phreatoicid and Gammarid fauna, and may be representatives of a palaegenic Gondwanic fauna; but too much must not be presumed from this association without further evidence. The above-mentioned *Jaera guernei* from the Azores does not weaken the case, as it is clearly a comparatively recent immigrant.

Family JAERIDAE.

In October 1916, Mr. A. T. Prentice of Somerset West sent me a tube-full of *Phreatoicus* which he had collected for me on one of his mountaineering excursions. By a fortunate chance and quite unwittingly he had collected also a single female specimen referable to this family. The following year I took the opportunity of visiting the exact spot in company with Mr. H. V. Begley, Mr. Prentice's constant mountaineering companion, and succeeded in obtaining specimens of both sexes.

As was to be expected, the animals were not at all rare, but from their small size were exceedingly difficult to find. Consequently it may prove useful to future collectors, both in this country and elsewhere, to detail the method which was found successful.

Failing to find any animals by looking with the naked eye or with a hand lens amongst handfuls of moss, a quantity of moss was collected into a tin without wringing it out, but merely draining off the superfluous water. It is important to choose not the *bright* green moss, but the dark more or less submerged clumps. After a short while the tin was filled up with water and the moss gently pressed and kneaded until the water was black and muddy, when numbers of the animals were seen floating about. The liquid can then be poured through a very fine sieve and the filtrate preserved for examination at home. As, however, the water contains so much vegetable debris and humic matter the filtering may be omitted, merely pouring off the muddy water, though, of course, rather more preserving fluid is required. The moss may be carried home or to camp if the weather be cool, but the preservation should not be delayed until the next day if possible.

The nature of the locality may be briefly indicated. (Pl. VIII, fig. 1.) The streamlet is a small tributary of the Kogelberg stream which falls into the Steenbras. It rises in a plateau between projecting kopjes and has a very gentle gradient until it joins the Kogelberg stream. In its upper reaches it meanders slightly and its source is undiscoverable among more or less marshy ground. In the dry season it never dries up completely owing to the thick vegetation and the frequency of the S.E. mists.

The animals are found only in these upper reaches. Lower down, where a moderately rapid current runs over a rocky or sandy bed, none are to be found.

Associated with them in the Sphagnum moss were numbers of a blind *Gammarus* and a local variety of *Phreatoicus capensis*, the latter especially being exceedingly abundant.

The present occurrence is thus exactly comparable with that of the Australian *Heterias* which Sayce discovered in company with a blind *Gammarus* and a blind Phreatoicid. Although too much importance may be easily attached to this association, yet it may afford us a very valuable clue to discovering further examples of freshwater Jaerids (and other Crustaceans) in other regions. Gammarids and *Phreatoicus* are comparatively easy to "spot" wherever they occur, and, when found, the above or a modified method should always be tried in the hope that the third party may also turn up.

Protojanira, n.g.

Body rather elongate, without sexual dimorphism. Corneal lenses and pigment completely absent. Lateral margins of the segments entire. First antenna with reduced flagellum, not multi-articulate. Second antenna with scale on 3rd joint. Outer and middle lobes of second maxilla apparently with simple setae. Maxilliped with 2nd and 3rd joints of palp not greatly enlarged. Peraeopods all similar, the first a little shorter and stouter, biunguiculate. Four pairs of oostegites, the 1st not folded as in *Asellus*. First pleopods in ♂ consisting of a short and broad basal part (fused peduncles) and two large foliaceous rami forming a protective covering over the other pleopods. Second pleopods in ♂ normal, but not taking part in the formation of the operculum, mostly concealed by the rami of the first pleopods. Operculum in ♀ normal, concealing the other pleopods. Pleopod 3 not larger than the first, inner ramus obscurely 2-jointed, outer ramus distinct. Fourth pleopod with 2 rami; 5th pleopod with 1 ramus. Uropods elongate, outer ramus longer than inner. Embryo without dorsal appendages. Freshwater.

It will be noticed that this genus resembles *Heterias* Richardson (1904, Pr. U.S. Nat. Mus., vol. xxvii, p. 6, nom. nov. for *Janirella* Sayce, nom. preocc.) in being totally blind, in the reduced flagellum of the 1st antenna, and in the non-specialised peraeopods.

In the character of the 1st pleopods, however, it is distinct not only from *Heterias*, but from all the known genera of the family.

This appendage recalls very strongly that of the allied family *Stenetriidae* in that the peduncles are short and fused and the rami large and well

developed. In *Stenetrium* the two peduncles are completely fused without trace of suture, but the rami are distinctly articulated to their respective peduncles. Here, on the other hand, there is a faint indication of a suture between the two peduncles, but none between the peduncles and the rami.

This apparent likeness to the *Stenetriidae* is at once discounted by the 3rd pleopods, which are typically Jaerid in structure, i.e. are not larger than the preceding pleopods and do not form an operculum. Also the operculum in the ♀ is formed by the large fused 1st pleopods, not by the 3rd pleopods. So that there is no question that possibly we are dealing with a freshwater Stenetriid.

The shape of the 1st pleopods in the ♂ must therefore be otherwise explained. Is it a degenerate condition? Or can it be a primitive feature, a stage in the evolution of the modern typical Jaerid structure from the ancient generalised type of pleopod?

If the first alternative be true, it means that the work of generations in bringing about the fusion of the peduncles is being undone. In favour of this is the complete absence of suture between the peduncle and ramus, suggesting that the whole represents the peduncle and never was divided; all trace of the ramus which would be at the distal end having disappeared, as in e.g. *Eurycope*. Against this view is the breadth of the appendage and the foliaceous nature of the "rami," both of which characters we must suppose in this case to have been reacquired after passing through the narrow condition found in all modern representatives.

This seems a little improbable, and moreover it is surely simpler to regard the second alternative as the true explanation. The short basal portion represents the fused peduncles, which are no longer (or very little) than in the 3rd–5th pleopods, which, from the general similarity throughout all classes of Isopods, admittedly resemble the primitive generalised type of abdominal appendage. The narrowing of the peduncles in the *Jaeridae* is correlated with the lateral displacement of the 2nd pleopods to help form a protective operculum. But in the present case the 2nd pleopods have suffered scarcely any displacement, being covered by the 1st pleopods to a much greater extent than in any other known Jaerid.

Further, in the 2nd pleopods the outer ramus is far better developed than usual; its degeneration into a mere "coupling hook" being by no means complete. In fact it *appears* to be 2-jointed, but this may be due to crumpling in preservation.

Therefore in these three features—namely, breadth of peduncles and rami of 1st pleopods, feeble lateral displacement of 2nd pleopods, and relative small degeneration of the outer rami of these latter pleopods—we seem to see evidence of a more or less primitive condition through which the ancestors of the modern *Jaeridae* probably passed, and which

we see still preserved in the other modern families of the *Asellota*, the *Asellidae*, and *Stenetriidae*.

But a further point crops up. According to Hansen (**17**, p. 310), whose interpretation seems to be generally accepted, the 1st pleopods in the *Jaeridae* consist of the fused elongate peduncles and a small more or less distinct terminal ramus. Why should the peduncle have become elongated? Though the question may not be answered, it is well to consider whether the present genus does not indicate another interpretation.

As stated above, there is not the slightest trace of a division between the basal part (peduncle) and the free lobe (ramus). We have only to complete the fusion of the two appendages along the middle line to obtain the elongate " peduncle " of typical Jaerids. So that the " peduncle " of Hansen may really be peduncle *plus* the basal joint of the ramus, and his rudimentary ramus the 2nd joint of the ramus. Moreover, there is good reason to suppose that the " basal joint " was once composed of at least two articulations as in the 3rd and 4th pleopods in *Stenetrium*, and the 3rd–5th pleopods in *Asellus* at the present day.

It remains to be seen whether this interpretation of the 1st pleopods will hold good. There are probably other minute forms awaiting discovery which may throw more light on the problem. The name of the new genus is chosen in reference to the supposed clue to the evolution of the 1st pleopods in the *Jaeridae*.

Protojanira prenticei, n. sp.

Text-figs. 8, 9.

Body elongate, parallel-sided, without sexual dimorphism, except that the ♀ is a little broader across the segments bearing the brood lamellae. Head about as long as broad or a little shorter, lateral margins minutely crenulate, and sparsely setose. Eyes completely absent. Peraeon segments broader than long, lateral margins finely crenulate, setose. Pleon as broad as long, suboval, margins finely crenulate, setose. Side-plates indistinguishable.

First antenna not much longer than head, flagellum 6-jointed.

Second antenna ⅗ length of body, 3rd joint of peduncle twice length of 4th, with distinct movable linear scale, tipped with 3 setae, on middle of outer margin, flagellum multi-articulate.

Mouth parts normal. Outer and middle lobes of 2nd maxilla appear to be tipped with simple setae. Maxilliped with 2nd and 3rd joints of palp not greatly expanded, epipod ovoid, outer margin not angular.

Peraeopods all similar, but 1st a little shorter and stouter. In 1st peraeopod 5th joint narrow-oval, with 4 spinules on inner margin, 6th as long as, but a little narrower than, 5th, with 2 subapical spinules on inner

margin, 7th equal to width of 6th, biunguiculate, with a seta between the two ungues. In the other peraeopods 5th and 6th joints distinctly linear and longer, nearly equal to 2nd.

First pleopod in ♂ consisting of a broad short basal piece with a faint median suture, bearing two broad foliaceous sub-quadrangular rami, twice

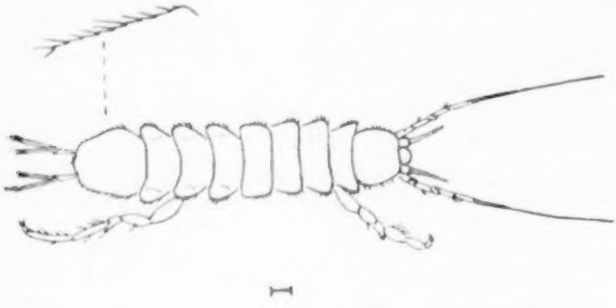


FIG. 8.—*Protojanira prenticei.* Whole animal enlarged, with line (n.s.) representing natural size. All peraeopods except two omitted. Portion of lateral margin of telson further enlarged.

as long as broad, forming an operculum covering the other pleopods, distal margins sparsely setose.

Operculum in ♀ as broad as long, rounded-quadrate, distal margin with a slight emargination.

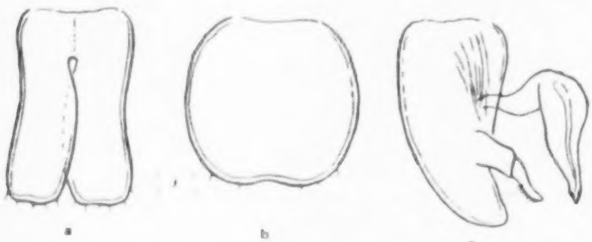


FIG. 9.—*Protojanira prenticei.* a, 1st pleopods ♂; b, operculum ♀; c, 2nd pleopod ♂.

Second pleopod in ♂ mostly concealed by the 1st pleopod, peduncle rather pear-shaped, apex blunt, inner ramus strong, its 2nd joint proximally broad and ending in a sharp point, with internal canal, outer ramus stronger than usual, apparently 2-jointed, but this appearance may be due to crumpling in the preservative, the proximal part stout, the distal narrower, with some excessively minute recurved setae.

Third pleopod, outer ramus ovate, obscurely 2-jointed, inner ramus distinct, apically blunt.

Fourth and fifth pleopods normal, outer ramus unjointed.

Uropods as long as pleon, peduncle shorter than the rami, of which the outer is a little longer than the inner. This feature is unusual, but is constant in all the specimens.

Length.—2·5 mm. ; *breadth*, ·5 mm.

Colour.—White.

Locality.—Streamlet on north side of Kogelberg, Hottentots Holland Mountains, Caledon Division ; 1 ovigerous ♀, October, 1916 (A. T. Prentice) ; ♂♂, ovigerous ♀♀ and juv. 1st October, 1917 (K.H.B.), (S.A.M., Nos. A4184 and A5172).

III. The Amphipodan Fauna.

Since the description of the four Table Mountain species in 1916 several opportunities have presented themselves of collecting in other localities. A number of fresh forms belonging to the "blind" group have thus been discovered, and the known range of the black-eyed Table Mountain form, *nigroculus*, has been extended.

Also many interesting data have forced themselves into notice concerning the habitats of these various forms.

A. Description of Species.

Key to the South African Species of Gammarus.

1. Eyes pigmented . . . . *nigroculus* Brnrd. and var. nov. *persetosus*.
2. Eyes not pigmented.
   - A. 4th side-plate strongly excavate posteriorly . *capensis* Brnrd.
   - B. „ „ quadrangular, not or only feebly excavate posteriorly.
     - 1. 4th side-plate longer than deep . . . *granulicornis* n. sp.
     - 2. „ „ deeper than long.
       - *a.* 2nd antenna ♂ with ear-like process on 3rd joint . . . *auricularius* Brnrd.
       - *b.* „ „ strongly setose . . . *seticornis* n. sp.
       - *c.* „ „ with strong spine on 4th joint . . . . *spinicornis* n. sp.
       - *d.* „ „ thickened.
         - i. 4th side-plate feebly excavate posteriorly . . . *tulbaghensis* n. sp.
         - ii. „ „ not excavate, considerably deeper than long *crassicornis* Brnrd.
       - *e.* 2nd antenna ♂ without particular features.
         - i. pale . . . . *kogelensis* n. sp.
         - ii. bright orange . . . . . . *aurantius* n. sp.

Accessory Branchiae.—These structures have been noted by Chilton in the Australian species *Gammarus barringtonensis* (**13,** p. 90, fig. 8). Their presence has been observed in several other families of Amphipods (see Chilton, Tr. Roy. Soc., Edinb., vol. xlviii, p. 472, 1912), but no definite conclusions have been reached as to their function. Chilton doubts their functioning as branchiae.

They have been found in all the South African species of *Gammarus*. They occur on all the peraeon segments except the 1st, and in both sexes. There is only one pair on the 2nd segment, but two pairs may occur on each of the following segments. In fact, in the larger species, *nigroculus* and *capensis*, there are as a rule two pairs on at least segments 3–5.

In the ♀ these structures on segments 2–4 are contained within the brood pouch.

Gammarus nigroculus Brnrd.

(1916. Ann. S. Afr. Mus., vol. xv, p. 206, pl. xxvii, fig. 23.)

Further localities for the typical form are as follows: Jonkers Hoek Valley, Stellenbosch; Witte River Valley, Wellington; French Hoek Pass; slopes of the Witzenberg Mountains in Tulbagh Valley; twenty-five miles east of Ceres on the farms Valsch Gat and Uitkomst; north slopes of the Langeberg Range east of Montagu; Cedarbergen, Clanwilliam. (All coll. K.H.B.)

Gammarus nigroculus Brnrd.

var. *persetosus* n.

Similar to the typical form in all respects except as follows:

Lower margins of side-plates slightly more setose. Antenna 1, accessory flagellum 4–5 jointed. Antenna 2 rather stouter, with 3rd–5th peduncular joints and the flagellum strongly setose in both sexes, in the ♂ the setae are especially numerous and long, forming a dense brush.

Peraeopods 1 and 2 in ♀ slightly more setose, in ♂ with dense fringe of setae on lower front margin of 2nd and posterior margins of 4th–6th joints, 7th joint with 5 (4 in French Hoek specimens) spines on inner margin instead of 3.

Peraeopods 3–5 also much more setose, especially in ♂, where there is a dense fringe on anterior margins of 2nd–6th joints and posterior margins of 4th–6th joints, posterior margin of 2nd joint also more thickly setose, 7th joint with 8–9 (6–7 in French Hoek specimens) spines on inner margin instead of 4–5.

Uropod 3 more setose.

Length.—Up to 15 or even 20 mm.

Colour.—Greyish, eyes black.

Locality.—Sneeuwgat Valley, south of the Gr. Winterhoek, Tulbagh District, alt. 4000–5000 ft., ♂♂ and ovigerous ♀♀, April and November, 1916, K.H.B.; French Hoek Pass, December 1916, K.H.B.; Zonder End Mountains, January 1919, K.H.B.; Swellendam Mountains, October 1925, K.H.B. (S.A.M., Nos. A4877–A4884, A4885, A6054, and A6936).

The above characters might be thought important enough to constitute a separate species.

Comparing a large series of the Tulbagh form with a similarly large series of the typical Table Mountain form, one notices firstly, that the dense fringes of setae on the 2nd antennae and the peraeopods in the former only attain their full development in large ♂♂, though these appendages in both the ♀♀ and the smaller ♂♂ are more setose than in the typical form; secondly, that in certain localities there is a tendency in the typical form to develop stouter 2nd antennae and more setose 3rd–5th peraeopods.

If to these considerations be added the fact that the typical form occurs in the Tulbagh Valley, separated by only one watershed from the Sneeuwgat Valley, the reason for instituting only a new variety, not a new species, will be clear.

Also some of the above characters are not constant. For example, the dactyli of the peraeopods in some specimens from Ceres, which otherwise resemble the typical form, have the same number of spines as found in the var. *persetosus*.

Gammarus capensis Brnrd.

(1916. Ann. S. Afr. Mus., vol. xv. p. 203, pl. xxvii, figs. 20–22.)

Syn.: ***Paramelita ctenodactyla*** Schellenberg, Deutsch. Südpol. Exp., xviii, p. 367, fig. 57, 1926.

The only locality outside the Cape Peninsula where I have found this species is in the Cedarbergen, Clanwilliam District (September 1923). The specimens are smaller than the average size of the Peninsula form, but are not otherwise distinguishable.

Gammarus auricularius Brnrd.

(1916. Ann. S. Afr. Mus., vol. xv, p. 209, pl. xxvii, figs. 26–28.)

An interesting point, which was not emphasised in the original description, is the *subchelate character of the 1st peraeopod in the ♂*. The 6th joint closes tightly against the 5th, and moreover both joints are bent outwards at right angles to the 4th joint.

Both the 5th joint of the 1st peraeopod and the "ear" on the 2nd antenna are frequently much more strongly developed than in the figures

I have given; the "ear" on the antenna often reaches to the end of the 4th peduncular joint.

Gammarus tulbaghensis, n. sp.

(Plate X, figs. 5, 15.)

Head not quite equal to first 2 peraeon segments. Antero-lateral lobes rounded-truncate. Eyes pale glistening when alive, invisible after preservation in spirit. Side-plates 1–3 as deep as their segments, deeper than long, subrectangular with rounded setose inferior margins, 4 deeper than long, inferior margin rounded, setose, posterior margin with a distinct though shallow emargination (Plate X, fig. 5). Pleon segments with only a very few setae on posterior margins, except on segments 4–6, where they are slightly more numerous, no spines on 6 at base of telson, postero-inferior angle of 3 rounded quadrate.

Telson $\frac{2}{3}$ as long as basal width, cleft almost to base, lobes not very dehiscent, apices rounded, with 3–5 setae and 1 spine, the latter being often absent.

First antenna in ♂ reaching 6th peraeon segment, 1st joint moderately stout, 2nd $\frac{3}{4}$ 1st and more slender, 3rd $\frac{1}{2}$ 2nd, flagellum a little longer than peduncle, 18–22-jointed in ♂, 17–19 in ♀, accessory flagellum 3-jointed; in ♀ rather shorter, 1st and 2nd joints shorter and more slender.

Second antenna in adult ♂ reaching to about middle of flagellum of 1st, stout, gland-cone not prominent, 3rd swollen but not as wide as long, 4th also swollen, 3 times as long as broad, with a low ridge on the basal part of the lower inner margin, 5th at right angles to 4th, $\frac{3}{4}$ length and $\frac{1}{2}$ width of 4th, flagellum longer than 5th but shorter than 4th, 9–11 jointed; in ♀ and immature ♂, rather shorter and much more slender, not stouter than 1st, 5th slightly shorter than 4th, flagellum ca. 10-jointed.

Mandibles with 2nd and 3rd palpal joints subequal.

First and second gnathopods, 6th joint oblong, longer in 2nd than 1st, not widening distally, palm transverse, defining angle with 3 spines, palm and hind margin setose; 2nd gnathopod stronger than 1st, and stronger in ♂ than ♀.

First and second peraeopods sparsely setose, anterior apex of 4th joint, hind margin of 5th and 6th each with three groups of spinules, of 7th with 2 distal spinules.

Third to fifth peraeopods not very setose, 2nd joint not strongly expanded, anterior margin spinulose, hind margin slightly serrate, setose, 7th (excluding unguis) $\frac{1}{3}$ length of 6th, anterior margin of 6th with three groups of spines, of 7th with 3 (peraeopod 3) or 4 (peraeopods 4 and 5) distal spinules.

First uropod, upper margin of peduncle with 4 spines, rami subequal.

Second uropod, upper margin of peduncle with 3 spines, outer ramus shorter than inner.

Third uropod not extending far beyond 1st and 2nd, peduncle with 2 apical spines, outer ramus twice length of peduncle, with 2 marginal groups of spines and setae, apex with a group of several spines, 2nd joint obsolete, inner ramus quarter length of outer, with 2 apical spines and a seta.

Length.—5–6 mm.

Colour.—Whitish, eyes white glistening.

Locality.—Sneeuwgat Valley, Tulbagh. Altitude ca. 4000 feet. In moss in a marshy place on the side of the hill above the main stream. April and November 1916, K.H.B. ♂♂ and ovigerous ♀♀. (S.A.M., No. A4875.)

This species bears a strong resemblance to the Table Mountain species *G. crassicornis*, but is distinguished by the less strongly incrassate 2nd antenna in the ♂, the 4th side-plate, and the finger of the three posterior peraeopods, as well as by other more detailed characters.

Gammarus seticornis, n. sp.

(Plate X, figs. 7, 17.)

Head rather shorter than first 2 segments. Antero-lateral angles rounded truncate. Eyes glistening white when alive, becoming invisible in spirit. Side-plates 1–3 almost as deep as their segments, deeper than long, subrectangular, with rounded setose inferior margins, 4 slightly deeper than long, inferior margin rounded, setose, posterior margin with shallow but distinct emargination. (Pl. X, fig. 7.) Pleon segments very feebly setose, chiefly on segments 5 and 6, no spines at base of telson, postero-inferior angle of 3-rounded quadrate.

Telson $\frac{2}{3}$ as long as basal width, cleft almost to base, lobes not very dehiscent, apices rounded, with 3–4 setae and a spine.

First antenna reaching 6th or 7th peraeon segment, 1st joint not stout, 2nd $\frac{2}{3}$ length of and slightly more slender than 1st, 3rd $\frac{1}{2}$ 2nd, flagellum longer than peduncle, ca. 25-jointed in ♂, 20 in ♀, accessory flagellum 4-jointed.

Second antenna (Pl. X, fig. 17) only slightly stouter than first in both sexes, reaching half way along flagellum of 1st, 4th joint not twice length of 3rd, 5th shorter and rather more slender than 4th, flagellum shorter than peduncle, ca. 12-jointed, in adult ♂ apex of 3rd, whole of 4th and 5th joints and flagellum densely clothed on lower surface with long simple setae, in ♀ and young ♂ only feebly and normally setose.

Mandibles with 3rd palpal joint very slightly shorter than 2nd.

First and second gnathopods, 6th joint oblong, longer in 2nd than 1st, not widening distally, palm transverse in 1st, slightly oblique in 2nd, defined by 2–3 spines, palm and hind margin setose; 2nd gnathopod stronger than 1st and stronger in ♂ than ♀.

First and second peraeopods sparsely setose, anterior apex of 4th joint slightly projecting, 6th shorter than 4th, hind margin of 5th with 3, of 6th with 2 groups of spinules, of 7th with 3 distal spinules.

Third to fifth peraeopods not very setose, 2nd joint not widely expanded, anterior margin spinulose, hind margin with a few widely spaced and very shallow setiferous serrations, the setae short, 7th (excluding unguis) ½ length of 6th, anterior margin of 6th with three groups of spinules, of 7th with (sometimes as in A5772 with 5) spinules distributed along the whole margin.

First uropod, upper margin of peduncle with 4–5 spines, rami subequal.

Second uropod, upper margin of peduncle with 2 spines, outer ramus shorter than inner.

Third uropod not extending very far beyond 1st and 2nd, peduncle with 3 apical spines, outer ramus twice length of peduncle, with 2 groups of spinules and setae on outer, 1 on inner margin, apex with a group of spinules and rather long setae, 2nd joint very small or obsolete, inner ramus ½ length of outer, with 1–2 apical spinules and a seta.

Length.—5–6 mm.

Colour.—Whitish, eyes glistening white.

Locality.—Hottentots Holland Mountains, Caledon side, Sneeuwkop, Landrost Kloof and various places in the Steenbras Valley. At mouth of Steenbras River just above high-water, west of Kogelberg. In moss in small springs and runnels on the sides of hills above, but not in, the main stream. Altitude from just above high-water mark to 4500 feet. On west slopes of Sir Lowry's Pass in Hottentots Holland above Somerset West. January 1916, K.H.B.; October 1916, A. T. Prentice, ♂♂ and ovigerous ♀♀. (S.A.M., Nos. A3994, A4003, A4004, A4061, A4872, A5175.)

A species resembling *G. tulbaghensis* in the shape of side-plate 4, but distinguished by the setose 2nd antenna in ♂, and the number of spinules of the 7th joints of the peraeopods in both sexes.

Gammarus kogelensis, n. sp.

(Plate X, figs. 9, 21.)

This species is closely allied to *seticornis*, but may be considered specifically distinct on account of the following characters which are constant.

Telson nearly as long as basal width, cleft almost to base, apices of lobes rounded, with a spine and 3–4 setae not very dehiscent.

Second antenna (Pl. X, fig. 21) not much stouter than 1st, reaching from ½ to ¾ along flagellum of 1st, or sometimes in ♂ about as long as 1st, 4th joint more than twice (2½) length of 3rd, 4th and 5th subequal, sparsely setose, flagellum shorter than peduncle, ca. 15-jointed, each joint with a rather dense whorl of setae, but the setae not forming a brush on the lower surface as in *seticornis*.

First and second peraepods, 6th joint as long as 4th, hind margins of 5th and 6th more strongly setose, the spines on the other hand less prominent, 4 on 5th, 5 on 6th, 7th with 4 spinules.

Third to fifth peraeopods, 2nd joint with hind margin distinctly serrate, with *long* setae arising from the serrations, anterior margin of 6th with 6 groups of spines, of 7th with 6–8 spinules. The whole limb more setose and spinulose.

Third uropod, peduncle with 6 apical spines, outer ramus with 3 groups of spines on outer, 2 on inner, margin, inner ramus ¼ length of outer.

In other respects similar to *seticornis*.

Length.—♂ 8 mm.; ♀ 6 mm.

Colour.—Pale yellowish or whitish, eyes glistening white.

Locality.—Hottentots Holland Mountains (in streamlets flowing down north and west slopes of Kogelberg, and west slopes of mountains between Kogelberg and Rooells River). ♂♂, ovigerous ♀♀. October 29, 1916, A. T. Prentice; October 1, 1917, K.H.B. and February 3, 1922, K.H.B. (S.A.M., Nos. A4873, A5174, A5190.)

Gammarus aurantius, n. sp.

(Plate X, figs. 6, 16.)

This species is so similar to *seticornis* that it will be enough to mention the differences.

The chief of these is in the 4th side-plate (Pl. X, fig. 6), which is deeper than long, the posterior margin with scarcely perceptible emargination, as in *crassicornis*.

Antenna 2 (Pl. X, fig. 16) in ♂ only slightly stouter than 1st, 4th joint at least twice length of 3rd, neither peduncle nor flagellum strongly setose.

Peraeopods 3–5, 2nd joint with more numerous setiferous serrations on hind margins, 7th joint half length of 6th, its anterior (inner) margin with 4–5 spinules in peraeopod 3, 6–7 in 4, and 8–9 in 5.

Length.—6–7 mm.

Colour.—Bright orange.

Locality.—Hottentots Holland Mountains, Caledon side, Landrost Kloof and Valley north of Vallei Berg. In moss in the meandering upper reaches of one of the tributaries of the main stream. January 1916 and

April 1917, A.T.P. and K.H.B. ♂♂ and ovigerous ♀♀. (S.A.M., Nos. A3997, A4005, A4869.)

Gammarus spinicornis, n. sp.

(Plate X, figs. 8, 18, 19.)

Head only a very little shorter than first 2 peraeon segments together. Anterior lobes rounded-quadrate. Eyes pale glistening when alive, in visible after preservation. Side-plates 1–3 as deep as their segments, deeper than long, inferior margin rounded, setose, 4 deeper than long, postero-lateral angle well marked, hind margin distinctly though not deeply excavate, inferior margin rounded, setose (Pl. X, fig. 8). Pleon segments 4–6 sparsely setose on hind margin, no spines on 6 at base of telson, postero-inferior angle of 3 quadrate.

Telson as long as broad, cleft to base, lobes broadly and symmetrically rounded apically, not very dehiscent, with a spine and 2–3 setae near outer distal margin.

First antenna rather more than half length of body, 1st and 2nd joints subequal, second more slender, 3rd ½ 2nd, flagellum longer than peduncle, ca. 40-jointed, accessory flagellum 4-jointed.

Second antenna (Pl. X, figs. 18, 19) in adult ♂ reaching at least half-way along flagellum of 1st, stout, 3rd joint short and broad, 4th reaching to end of peduncle of 1st, thrice as long as broad, lower outer apex produced in a strong forwardly directed tooth, on upper margin of which is a very faint indication of a secondary tooth, 5th shorter than and only half as wide as 4th, closing on inside of tooth on 4th, flagellum scarcely as long as peduncle, ca. 15-jointed, both peduncle and flagellum sparsely setose; in ♀ not stouter than 1st, 5th only slightly shorter than 4th, flagellum shorter than peduncle, ca. 15-jointed.

Mandibles with 3rd palpal joint scarcely as long as 2nd.

First and second gnathopods, 6th joint oblong, palm slightly oblique, setose defining angle with 3–4 spines, hind margin not densely setose, finger matching palm. Second gnathopod rather stronger than 1st, both stronger in ♂ than ♀.

First and second peraeopods sparsely setose, anterior apex of 4th, 5th, and 6th joints each with four spines (♂) or spine-setae (♀) on hind margin, 7th with 4 spinules along inner margin.

Third to fifth peraeopods not strongly setose or spinose, 2nd joint not strongly expanded, anterior margin spinulose, third margin slightly serrate, setose, anterior margin of 6th with 4 groups of spines, 7th (excluding unguis not quite ½ length of 6th, inner margin with 6–8 spinules.

First uropod, upper margin of peduncle with 4 spines, rami subequal.

Second uropod, upper margin of peduncle with 3 spines, outer ramus slightly shorter than inner.

Third ramus not extending far beyond the others, peduncle with 6 apical spines, outer ramus not quite twice length of peduncle, with 3 marginal groups of spines, 2nd joint small, surrounded by 2–3 spines and a few setae, inner ramus ⅓ length of outer, tipped with 3 spines and a setae.

Length.—♂ 8 mm.; ovigerous, ♀ 6–8 mm.

Colour.—Pale brown.

Locality—Hottentots Holland Mountains (Valley of the Steenbras stream where it crosses Caledon road, 1300 feet; mountains above that spot, 1600 feet, in stream falling over escarpment into Somerset West basin; on hillsides above Government plantations and in stream draining into Palmiet from Spitzkop, up to 2200 feet). November 1916 and October 1917, ♂♂ and ovigerous ♀♀, K.H.B.; Zonder End Mountains, 3500–4500 feet, January 1919, ♂♂ and ovigerous ♀♀, K.H.B.; Langebergen, near Swellendam, Zuurbrak and Tradouw Pass, 3000–5000 feet, October 1925, ♂♂ and ovigerous ♀♀, K.H.B. (S.A.M., Nos. A5177, A5179–81, A5186–87, and A6939–43.)

In the specimens from the valley of the Steenbras, 1300 feet, the tooth on the 4th joint of the 2nd antenna of ♂ is more slender and there is sometimes a low rounded knob on the lower *inner* margin near the base. In the stage which appears to precede immediately the final moult, there is a small setiferous protuberance in the place where the tooth will be.

Gammarus granulicornis, n. sp.

(Plate X, figs. 10, 11, 20.)

Head not equal to first two peraeon segments. Anterior lobes rounded quadrate. Eyes glistening white when alive, invisible after preservation. Side-plates 1–3 scarcely as deep as their segments, 1 about as deep as long, 2 and 3 longer than deep, inferior margin not strongly rounded, setose. 4 similar to 3, longer than deep in ♂, in ♀ scarcely as deep as long, subquadrangular, hind margin straight, lower margin feebly rounded, setose (Pl. X, figs. 10, 11). Pleon segments 4–6 sparsely setose, no spines on 6th at base of telson, postero-inferior angle of 3 rounded-quadrate.

Telson broader than long, cleft nearly to base, lobes apically rounded truncate not dehiscent, 1 spine and several setae on outer distal margin.

First antenna ⅔ length of body, 2nd joint slightly shorter and more slender than 1st, 3rd ½ 2nd, flagellum longer than peduncle, ca. 40-jointed, accessory flagellum 5-jointed.

Second antenna (Pl. X, fig. 20) in adult ♂ reaching half-way along flagellum of 1st, moderately stout, 4th joint reaching to end of 2nd joint

of 1st antenna, about thrice as long as broad, both inner and outer margins on lower surface slightly keeled, each keel with 4 tiny setiferous granules, 5th shorter and rather more slender than 4th, inner margin on lower surface keeled, with 5 tiny setiferous granules or serrations, flagellum about as long as peduncle, ca. 16-jointed, each joint with several short setae. In ♀ not thicker than 1st, 5th joint slightly shorter than 4th, flagellum ca. 12-jointed.

Mandibles with 3rd palpal joint almost as long as 2nd.

First and second gnathopods in ♂ large in proportion to size of animal, 6th joint oblong, robust in 2nd gnathopod, palm slightly oblique, convex, defining angle forming in 2nd gnathopod a small projecting rounded tooth, with 3 spines at its base, in 1st gnathopod not projecting, inferior margin slightly crenulate, with tufts of setae, finger matching palm, in 2nd gnathopod reaching to but not overlapping defining tooth; in ♀ very much less robust, not unusually large, defining angle in 2nd gnathopod without projecting tooth.

First and second peraeopods in ♂, 2nd joint with hind margin rather strongly spinose, 4th rather strongly expanded distally, 5th abruptly narrower and very noticeably shorter than 4th, its hind margin with 3 spines, 6th slightly longer than 5th, hind margin with 4 groups of spinules and setae, 7th including unguis ½ 6th, inner margin with 3 spinules; in ♀ much more slender, 2nd joint not strongly spinulose, 4th not unusually expanded distally, 5th not very much narrower than 4th, 7th with 2 spinules on inner margin.

Third to fifth peraeopods not strongly setose or spinose, 2nd joint not strongly expanded, anterior margin spinulose, third margin very feebly serrulate, setulose, anterior margin of 6th with 3 groups of spines, 7th with 5–7 spinules on distal portion of inner margin.

First uropod, upper margin of peduncle with 4 spines, rami subequal.

Second uropod, upper margin of peduncle with 3 spines, outer ramus slightly shorter than inner.

Third uropod not extending far beyond the others, stout, peduncle with 4 spines on apical margin, outer ramus twice length of peduncle, thrice as long as wide, margins with 2 groups of spines, apex truncate, spinose, 2nd joint obsolete, inner ramus ½ length of outer, tipped with 2 spines and a seta.

Length.—♂ 8 mm.; ovigerous ♀ 6–7 mm.

Colour.—Whitish.

Locality.—Hottentots Holland Mountains (in same localities and occurring together with the preceding species). ♂♂, ovigerous ♀♀. November 1916 and October 1917, K.H.B. (S.A.M., Nos. A4874, A5178, A5182–85.)

This species is remarkable for the shape of the 4th side-plate. Dis-

tinctive also are the 2nd antennae in ♂, the hand of the 2nd gnathopod in ♂, and the relations between the 4th and 5th joints of 1st and 2nd peraeopods.

B. *The Structure of the Eye in the "Blind" Species of* Gammarus.

The South African species of *Gammarus* present two very distinct types of eye. The one is a deeply pigmented black eye like that of *G. pulex* and other species, the pigment of which is insoluble in the ordinary preserving fluids. The other is an unpigmented glistening white eye, which after death becomes dull white, and after a few hours or days in preservatives disappears so completely that, externally examined, it would be thought to be absent altogether.

In the following pages are detailed the results of an histological examination of the second type of eye.

The first type of eye, which is found in *G. nigroculus*, I have not specially studied beyond determining that it is a normally constructed, functioning eye, comparable with that described by Parker (**25**).

The degenerate eyes of European and American species of Gammarids have been examined by Parker (**25**), Della Valle (**16**), Vejdovsky (**42**), and others. Strauss (**38**) gives a useful summary, and has confirmed and extended the work of earlier workers.

Material and Methods.—Since no further mention will be made of the eye structure in *G. nigroculus*, it will suffice to say here that in depigmenting sections the usual reagents, such as potassic hydrate, and alcohol and nitric acid, work well.

For the study of the other species of *Gammarus*, specimens were preserved in 70 per cent. alcohol, alcohol and acetic acid, corrosive-acetic, Bouin's solution, and Mayer's picro-nitric. Fair results were obtained with all these fluids, but the alcoholic ones proved the best and gave most satisfactory results.

I can strongly recommend Strauss' mixture of alcohol and acetic acid (97 parts of 96 per cent. alcohol and 3 parts of glacial acetic). Besides preserving the structure perfectly, it has the great advantage of causing the cuticle to separate entirely from the underlying tissues. The shrinkage whereby this is effected is very slight, and in no way alters the essential shape of the cells. If the antennae and mouth-parts be removed after fixation, it will be found that with a little manipulation the whole cuticle can be stripped off the head, and the sections can then be cut without the usual trouble of softening the chitin.

It is advisable first to cut off the head of the living animal and then place direct in the fixative. Fixation is complete after an hour, but there

is no harm in leaving the heads in until wanted. Haematoxylin was found to be the best stain.

External Appearance.—Reference to the external appearance was made in the original descriptions of the species (Barnard, **5**, pp. 203, 207, 209). In the living animal the "eye-spots" are glistening white or very pale pink. This glistening appears to be due to the light reflected through the cuticle from the opaque white cells below. After death the glistening soon disappears, and the eye-spot becomes dull white.

The eye-spots are round-oval in shape, quite regular, and show only a very slight decrease in proportional size when compared with the normal eyes of *G. nigroculus.*

After about a week in alcohol, formalin, or corrosive-acetic, all trace of this white eye-spot is removed, and the specimens would be described as absolutely blind. In the two solutions containing picric acid, however, all external trace of the eyes has disappeared within 12 hours.

Histology.

(*a*) *G. capensis.*

(Plate XI, fig. 1.)

There is no cuticular thickening over the eye.

The hypodermis covering the eye is in no wise different from the rest of the hypodermis, the cells not being in the least elongate.

The "eye-mass" is conical in shape, the oval base adjoining the hypodermis, the apex passing gradually into the optic nerve. It is bounded by a distinct capsular or bounding membrane, which, however, I have failed to trace through the optic nerve.

The optic nerve is well developed, and passes into a globular expansion of the cerebral ganglion. There is no optic ganglion distinctly cut off from the cerebral ganglion.

The conical eye-mass is composed of only one kind of cell. In horizontal or transverse sections these cells appear more or less elongate and irregularly spindle-shaped. In tangential sections they are far more irregular. Their boundaries are distinct. The nuclei are oval or round, but sometimes irregular, as if in process of degeneration.

Cone-cells, rhabdomes, and basement membrane (membrana fenestrata) are completely atrophied.

As to the nature of these cells composing the eye-mass, there are only two alternatives. They may be either the retinular cells, increased above the normal number, and consequently forced to take a more or less fusiform shape at various levels between the hypodermis and the optic nerve; or they may be the accessory pigment cells.

With regard to the first alternative, instructive comparisons can be made with *Stegocephaloides valdiviae*,* studied by Strauss (**38**, pp. 72, 73, figs. 44–46). Here large numbers of the nuclei of the retinular cells are heaped together at the proximal part of the eye.

Another example and one more comparable with our present case is *Cyphocaris richardi* (Strauss, **38**, p. 67, text-fig. 40, and pl. vi, fig. 37), in which spindle-shaped retinular cells are seen with their nuclei at various levels. This is especially noticeable in the young specimen (fig. 40). In this case, if we imagine the retinular cells increased in number, and at the same time the cone-cells to atrophy completely, we should have a condition exactly comparable with that found in our *Gammarus*.

But on the other hand it is the accessory pigment cells (Füllzellen of Strauss) which in the normal eye contain the " whitish opaque pigment " (Parker, **25**, p. 72). Analogy would suggest that the cells comprising the degenerate eye are to be identified as accessory pigment cells, since they also contain the white pigment ; and Strauss has recorded a case in which the great bulk of the eye is composed of large numbers of accessory pigment cells, viz. *Tryphosa kergueleni* (*loc. cit.*, p. 52).

No case has yet been recorded of the white pigment being found in the retinular cells. Strauss supposes that the very fleeting orange-yellow colour of the eye of *Cyphocaris richardi* is contained in the plasma of the Füllzellen (*loc. cit.*, p. 66).

Thus it would seem more correct to call the cells in question accessory pigment cells than to identify them with the retinular cells.

Della Valle does not state, in regard to *Niphargus puteanus* (=*elegans*), in what cells the yellow pigment is contained. There are no cells between the elongate hypodermis cells and the so-called " retinular ganglion." If the pigment is contained in the latter, the case is exactly comparable with the present one. In fact, one cannot help being struck by the great resemblance between Della Valle's figure 4† on plate liv and my figure (Pl. XI, fig. 1), barring the elongate hypodermis cells and the fewer nuclei in the " retinular ganglion " in the former.

(*b*) *G. auricularius*.

(Plate XI, fig. 2).

In general structure similar to *G. capensis*. The optic nerve, however, is shorter and much stouter. In fact, the connection between the cerebral mass and the eye might more properly be called the optic ganglion.

The eye-mass is proportionally larger than in *capensis*. Its component

* Not specifically diagnosed, name therefore a *nom. nud.*

cells are comparatively few in number, but much larger than those in *capensis*, but in size as well as in shape irregular. The nuclei are oval, without signs of degeneration.

This species is brown in colour, the pigment being contained in the hypodermis. The hypodermis covering the eye is slightly thinner than elsewhere, and contains no pigment.

I have also examined the eyes of *G. aurantius* and *spinicornis*, which are essentially of the same structure.

The White "Pigment" or Substance.—While the black pigment in the Crustacean eye is known to be a melanin, nothing on the other hand seems to be known concerning the chemical nature of the opaque white pigment. Nor am I able to add anything definite to our knowledge.

The only test which has been tried was one for lipochromes. The eyes of several freshly beheaded animals were dissected out, placed in absolute alcohol in a hollowed microscope slide and covered. After 24 hours the addition of a minute drop of potassium iodide gave a very faint blue reaction.

While this may possibly indicate that the pigment is a lipochrome, it by no means settles the question. Probably more definite results would be obtained by the employment of a greater quantity of the pigment extracted from some larger Crustacean.

As to the physiological use of this pigment for purposes of vision there are few references in the literature. Exner mentions a yellow substance of very high refractive index, which he calls a tapetum, and which he says evidently serves for refracting the light. This reflection is hindered at certain places by the development of the black pigment. As, however, I only know Exner's statements at second hand through Hess (Handb. Vergl. Physiol., 1912, Bd. 4), I can only presume that he is referring to the same white pigment as is found in the accessory pigment cells.

Hess's own researches on this tapetal substance showed that it was strongly fluorescent in ultra-violet light, and he believes that this fluorescence is due partly to the conversion of the very short violet and ultra-violet light-waves into greenish rays of longer length. These latter rays he states possess the greatest light-value (Helligkeitswert) for all the hitherto examined Crustacean eyes (*loc. cit.*, p. 771).

This may be the true physiology of the pigment in a normal functional eye: to strengthen the light falling on the retinulae, partly by direct reflection and deflection into a more suitable direction, and partly by converting it as far as possible into greenish light. But has it any functional value in the present case of eyes which have lost all the mechanism of vision? The optic nerves are still normal and presumably are able to convey impressions of light *intensity* to the brain. By far the greater part,

however, of the light falling on the eye-mass must be reflected. And the significance of what little does pass through as greenish rays is discounted by the fact that all the species are more or less negatively phototropic and live concealed during the day.

Thus we seem forced to the conclusion that the white pigment in the degenerate eyes has no functional significance at the present day. It, and the cells containing it, must be looked upon merely as the last remnants of the visual elements composing the eye.

The Causes of Degeneration of the Eye.—The only cause one can invoke apparently for the degeneration of the eyes is the habit of retiring deep down among the crevices of the rocks on the approach of dry weather. We cannot, however, describe the blind species as subterranean in the sense that the European *Niphargus puteanus* or New Zealand *Phreatogammarus fragilis* are subterranean. In the winter *G. capensis* can be found in open streamlets only just below the surface of the sand on the bottom or even swimming about in the open.

All the blind species are forced at the present day to descend more or less deeply below the surface on the approach of the dry season. To this must be attributed the degeneration of the eye.

There is some temptation to regard the blind species as older than the black-eyed *nigroculus*. But Allen and Sexton (**1**) in their Mendelian experiments have shown that in *G. chevreuxi*, not only the pigment, but even the structure of the eye, rapidly undergoes degeneration in the course of a few generations. One would not of course expect such a rapid atrophy under natural conditions, but the instability of the eye is a warning against the above assumption.

Further reasons are adduced below for *nigroculus* being the older species phyletically, and the blind species later modifications.

C. *Biology.*

The sole reason why the Gammarid (and Isopodan) fauna has remained unknown all these years seems to be due to collectors, e.g. Max Weber, having visited the larger rivers and paid attention chiefly to the larger forms, such as fishes, decapod Crustaceans, and Mollusca. And it is exactly in such situations that the Amphipods are absent.

My experience of the European freshwater Gammarids is too limited for drawing comparisons, but in England I have never found *G. pulex* except in small brooks, where there is neither a great volume of water nor a very swift current.

In South Africa very similar conditions appear to be necessary for *G. nigroculus*. Streams which are not so swift as to prevent the growth

of Sphagnum moss or other vegetation and the accumulation of vegetable debris are the only ones that offer prospects of a successful search. In all the districts hitherto explored all such streams may be termed mountain streams, being either within or in close proximity to the mountainous areas. When they reach the lower plains they have become far too formidable in bulk and velocity to form habitats for the animals.

In this respect the Sneeuwgat Valley at Tulbagh is instructive. This valley (4000 ft. alt.) is drained by several streams descending from the surrounding mountains (chiefly the Witzenbergen). The rainfall in winter must be considerable, and frequently the whole valley lies deep in snow. The main streams are in places open and about 4–5 feet across, with clear shingly or stony beds. In other places, where the vegetation is thicker, a stream appears to be only a foot or two across. But closer inspection shows that only the tops of the banks are that distance apart; farther below they are undercut to such an extent that the actual stream is as wide as the more open ones.

Evidently these streams are subject to winter floods and nowhere along them can any *Gammarus* be found. Only at their very sources, in some sheltered crevice, or in the numerous little tributary runnels which arise from the smaller kopjes and which are choked with *Sphagnum*, weeds, and debris, are the animals to be found, and here they are abundant.

The same remarks apply to the habitats of *nigroculus* in other localities. The two essential factors for this species are the presence of surface water throughout the year and the absence of liability to scouring winter floods, which would wash away the vegetable debris and deprive the animals of food and shelter.

In the Hottentots Holland Mountains we find *nigroculus* frequenting not so much the *Sphagnum* moss as the tufts of *Scirpus* grass which grow in the streams. This plant grows attached to stones, forming in time thick tufts and often, where the bed is shingly, cementing the stones together with a thick green carpet. The leaves are long and filimentous, affording excellent protection to the animals. A certain amount of decaying vegetable matter, derived from the plants themselves and from extraneous sources, is retained among the tufts, though not so much as in streams filled with *Sphagnum*.

Some of the " blind " species are found in very similar habitats. Thus *G. tulbaghensis*, *seticornis*, *aurantius*, *spinicornis*, and *granulicornis* frequent runnels and streamlets or marshy spots with plenty of humus, vegetable debris, and moss.

Some of the rills, e.g. in the Steenbras Valley, are known to dry up in the summer, and it is a point still to be determined whether the animals burrow down into the sandy bed and crevices of the rocks until they reach

a perenially moist stratum, or whether these rills are restocked at the beginning of the wet season by animals carried down by the overflow water from parts of the marshy ground which does not dry up. The latter is the more probable. I have tried to find the animals by digging during the dry season (March or April) in a place where previously in November I had found them plentiful, but without success. This point should be determined if possible by someone actually on the spot, for the rills dry up very rapidly once the dry season sets in.

In the case of *G. capensis*, however, on Table Mountain the animals do undoubtedly seek refuge in the joints and cracks of the rocks, working their way down until they come to the level of the perennial ground water. This is the only explanation for their reappearance year after year in some streams (e.g. one running through a small cave near the top of the Fountain Ravine) which flow on the surface only during the wet months.

It is supported also by the habitat of *G. crassicornis*, which is never found in proper streams, but only in the trickles on ledges or in tiny grottos on the escarpment cliffs of the mountain, where the water merely oozes out from between the clefts in the rocks.

These two species are thus able to maintain themselves in places where *nigroculus* is unable to do so, partly owing to the jointed and cracked nature of the rock, and also partly it seems to the former's ability to find a livelihood where there are only isolated particles of decaying vegetable matter, whereas *nigroculus* appears to need considerable quantities.

This fact is clearly seen at one place in the Platteklip stream on Table Mountain, where at about 1000 feet altitude the limits of *nigroculus* and *capensis* meet. The former lives in pools or hollows just beside the main stream where large quantities of leaves and other vegetable matter accumulate. But the latter lives only in the clearer parts of the stream, where the animals protect themselves from being washed down by getting under or between stones or burrowing in the sand.

It is difficult to say anything definite regarding the heliotropism of these animals. *G. nigroculus* seems to have no objection to light, for it can be seen clambering over and among the leaves, etc., even with the sun shining full on to the pool. On the other hand, *G. capensis* is only rarely seen moving about in daylight, and then only for brief moments in the course of its burrowing in and out of the sand or scuttling from under one stone to another. In the latter case the dislike to light may be more apparent than real, for when the animals come out into the open they are deprived of any objects to crawl against, and therefore propel themselves by movements of the pleon which results in a much more rapid progression.

These two species therefore, whose limits would be represented on a map as overlapping, are biologically completely separated by their habits.

This explains probably why in this spot I have never collected any hybrids or seen any pairing between the two species.

Moreover, *nigroculus* can be collected in numbers by sinking a scoop net on the bottom of the pool and placing inside it some fruit, such as apricot skins, when in a very short time the bait will be covered with animals. Specimens of *capensis*, however, have to be collected almost one by one. They will not come to bait, not even at night. In the Zonder End Mountains I have collected *G. spinicornis* in large numbers by leaving the porridge saucepan in the stream overnight.

Of the "blind" species, *auricularius* is perhaps the least heliophobic, as it is frequently to be seen crawling about amongst the moss or water-weeds near the surface of the water. Further reference will be made to it under heading of colouration.

Breeding Habits.—In strong contrast to *Phreatoicus*, which breeds only at one particular season of the year, the species of *Gammarus* breed nearly all the year round.

In the table below are indicated for the various species the months in which they have been found breeding. The first four are Table Mountain species, which are easy of access, and for them there are records for nearly every month. The other species are from localities farther afield, which have been visited only a few times at the seasons which are most propitious for exploring the mountain ranges.

The table, however, shows that breeding in some species (and probably in all) continues throughout the year.

Months . .	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	XI.	XII.
nigroculus .	×			×	×	×	×	×	×	×	×	×
capensis .	×	×	×	×	×	×	×	×	×	×	×	×
auricularius .	×	×	×	×	×	×	×	×	×	×	×	
crassicornis .	×	×	×	×	×	×	×	×	×			
spinicornis .	×									×	×	
granulicornis .										×	×	
aurantius .	×		×	×								
kogelensis .										×		
seticornis .	×									×		
tulbaghensis .				×								

Colouration.—*G. nigroculus* is of a brownish or greyish tint, not so dark but that the black humus-filled intestine shows through. The pigment is perfectly uniform. The darkest specimens appear to be found on the Peninsula, and some of the lightest come from the Hottentots Hollands.

In preservative the brown changes to an orange tint, and later both brown and grey tints fade completely to an opaque white.

All the blind species (except *auricularius*) may be described in general as colourless. They are of a translucent white with tinges of pale pink or cream. *G. aurantius*, however, is a bright orange. All tints fade in preservative to the same opaque white.

The colouration of *G. auricularius* is a light brown, the appendages being cream coloured. When seen under a lens, the brown colour appears as a very fine reticulation on a cream ground-colour, the reticulation being finer on the peraeon and pleon than on the head. The colour-pattern on the head is curiously like that on the head of *Phreatoicus capensis*, which may possibly indicate that the deposition of pigment is laid down in accordance with certain definite physiological causes.

At any rate the resemblance is noteworthy, and the deposition of pigment in a definite pattern is quite unusual or even, so far as I am aware, unique in a species of *Gammarus*.

Moreover, in contrast with the uniform and fleeting pigmentation of *G. nigroculus*, the pigment in *auricularius* is fast in preserving media.

Correlation between Structural Features and the Size and Periodicity of the Stream.—The term correlation is used advisedly, without any inherent idea of cause and effect. I know of no actual experiments designed to ascertain whether the volume of water has any effect on the size of the organism in the case of Crustacea, like those of Semper on Molluscs (**32**, p. 160). Thus the following associated facts, which are very noticeable, may be labelled correlations, although further observations may modify their significance.

(i) The size of the animal is directly proportional to the body of water in the stream, and the perennial character of that stream. Where there is a considerable body of water on the surface throughout the year, there the largest specimens will be found (*cf. G. capensis* from Platteklip stream and Waai Vlei). But where the surface water diminishes greatly during the summer months only dwarfed specimens are to be found (cf. *nigroculus* from Oranjezicht, Cape Town, and *crassicornis* in comparison with *capensis*).

The amount of food may of course be the prime factor determining the size. But as this is probably dependent on the quantity of water, in the case both of *capensis* and those species that feed on small particles, and of *nigroculus*, which prefers considerable accumulations of rotting leaves, etc., the correlation may still hold good.

A further example of this correlation is the common freshwater crab, *Potamonautes perlatus*, which in mountain streams only reaches a size of 1¼ inches, but in the larger rivers and vleis (e.g. on the Cape Flats) 3–4 inches across the carapace. The small forms are sexually mature.

A similar phenomenon was observed by Smith among the species of *Astacopsis* in Australia and Tasmania (**34**, pp. 146, 156). He suggests that young of the large forms in the rivers may be destroyed by predaceous fish, or alternatively that the population in the rivers is recruited from the mountain streams. In the case of the Cape *Potamonautes*, acquaintance with its habitats leads me to the conclusion that the latter alternative does not apply to this animal. The large and small forms in many places have no chance of mingling, and both forms may be found breeding. It is true the small forms appear to be rarer in the rivers, but that I believe is due not merely to greater conspicuousness but also to the fact that the young take more care to hide themselves.

(ii) Species or varieties with stout 2nd antennae are found only in the smaller runnels. Compare the thickening of the 2nd antennae in the forms of *capensis* as one proceeds southwards along the Peninsula, and the Oranjezicht form of *nigroculus*. Also *crassicornis*, *spinicornis*, and *tulbaghensis*.

On the other hand, exceptions to this rule are not unknown. *G. seticornis* is found in places where there is less water than where *spinicornis* is found, and yet the 2nd antennae are not noticeably thickened. Further, the *persetosus* variety of *nigroculus* has distinctly thickened antennae, but lives in streams not differing in size from those containing the typical form.

But in this latter case a close examination shows that both the typical form and the variety *tend* to develop thicker second antennae and greater setosity in the smaller streamlets.

The two extremes of this evolutionary tendency are represented by the large typical form of *capensis* found in proper streams, and the dwarfed *crassicornis* in the mere trickles and runnels. A certain allowance must be made, of course, for sex, since in the male the thickening process seems to have gone very much farther than in the female, which retains the more primitive features as in other classes of animals.

Evolutionary Tendencies.—This is really only another way of presenting some of the facts set out in the previous section. There a definite relation was sought between structure and physical environment, although in no case could actual cause and effect be shown.

The present point of view, however, places the facts in a more subjective light, regarding the development of certain structural features as due to some inner growth-trend or evolutionary tendency. It is another way of saying that we cannot discover any objective environmental cause to account for such features.

(*a*) The first of these characters is the shape of the 4th side-plate. In the great majority of *Gammaridae*, and, as far as I can discover, in every species of *Gammarus* except the Tasmanian *G. ripensis*, and some of the South African species, this plate has a very distinct postero-lateral angle,

above which the hind margin is distinctly and usually strongly concave. This concavity embraces the 5th side-plate.

How far is this character a guide to evolutionary status? The side-plates or epimera are regarded as developments of the coxae or 1st joints of the limbs; how far, if at all, the body wall enters into their composition need not be discussed here. The point is that at their inception they must have been developed as a series of *uniform* shallow outgrowths, the posterior ones perhaps arising later than the anterior ones. The protection afforded to the branchiae and the developing brood may have led to their gradual development, until in some forms (e.g. certain *Amphilochidae*) they form a protective shield into which the pleon, head, and all the appendages can be withdrawn, analogous to the bi-valve shells of Ostracods and Phyllopods.

Further, the specialisation of the 4 anterior side-plates seems to be correlated with the activity of the animal, for the great majority of the species with undifferentiated side-plates are domicolous (see key to families in Stebbing, Das Tierreich, 1906). Protection for the appendages and brood not being necessary in these families, they have retained to a large extent the shallow undifferentiated side-plates of the more primitive Amphipod. On the other hand roaming families, typified by the present-day dominant family of the *Lysianassidae*, possess deep, strongly developed side-plates.

The development of the triangular backward process of the 4th side-plate embracing the 5th is evidently an attempt to make up for the inability of this latter plate to expand. The 5th and 7th side-plates have perforce been restricted in their growth by the necessity of retaining freedom of movement for the 3 posterior peraeopods.

Thus it might seem permissible to regard the possession of a 4th side-plate similar in shape to the 3rd as evidence of primitiveness, although at the same time the possibility of its being a secondary development or degeneration from the specialised form must be borne in mind.

But assuming that we are dealing with no such secondary developments, what conclusions can we draw in regard to the South African Gammarids?

The "typical" 4th side-plate with postero-lateral angle and concave hind margin is found *fully developed* in only two species—*nigroculus* and *capensis*. One of these species is an eyed and the other a "blind" form, and both are the largest gammarids in the country. All the other species are "blind," and are mostly small. They show various stages in the development of the specialised side-plate from the quadrangular form. Or in other words, they have retained to a greater or less extent the (supposed) primitive form.

Thus *granulicornis* not only has a perfectly quadrangular 4th side-plate, but it is *longer than deep* (as are also side-plates 2 and 3), which on the view here taken betokens a very primitive condition. The series then

passes through *aurantius, crassicornis, aurcularius, spinicornis, tulbaghensis*, and *seticornis* (see Pl. X, figs. 1–11).

Are these forms the modern representatives of the ancestral fauna which are gradually developing towards the "typical" gammarid form, which only *capensis* has yet succeeded in reaching?

If the question be put in this way, it is obvious that *nigroculus* is regarded not as forming part of this so-called ancestral fauna, but as a more recent addition to the fauna. The topographical evidence (*infra*, p. 189) is, however, against this conclusion, and leads us to the above-mentioned alternative. On this theory *capensis* (and *nigroculus*) might be regarded as representing the original form, and the smaller present-day forms as so many stages in the simplification of the 4th side-plate.

Further, in *granulicornis* the 4th side-plate is slightly deeper in proportion to length *in the ♀ than in the ♂*. On the assumption that the female retains the ancestral features to a greater extent than the male, we can regard this species as evidence for the second alternative.

(*b*) The 2nd antennae. In the majority of Gammarids these are scarcely or only slightly thicker than the 1st antennae. The genus *Gammarus* as developed in other parts of the world is no exception. But in South Africa there is a very marked tendency for the 2nd antennae in the ♂ to become distinctly thicker than the 1st, carried in some cases to an extreme only paralleled elsewhere among the *Corophiidae*.

This thickening seems to be correlated with a decrease in the size of the animal which, as noted in the preceding section, is correlated with the smallness of the stream in which the animal lives. This is well seen in tracing *capensis* through the Peninsula southwards from Table Mountain. But in none of the forms of this species does it reach anywhere near the thickness found in *crassicornis* or *spinicornis*. In the latter the development of a spiniform tooth at the lower apex of the 4th joint renders the antennae exactly comparable with that of e.g. *Corophium grossipes* (Linne) (see Sars, Crust. Norw., 1, pl. 219), a most remarkable case of convergence.

But not *every* small species is characterised by stout 2nd antennae: *aurantius* and *seticornis* are exceptions.

Further, in *seticornis* we see another tendency in the ♂ in another direction: towards the development of a dense brush of setae on the distal peduncular joints and on the flagellum. This tendency is exhibited also by the black-eyed *nigroculus* (var. *persetosus*).

Thus it would seem that the development of brush-like 2nd antennae is *sui generis* and offers no clue to the evolution of the different species. But it is otherwise with the thickened antennae. For it seems plausible that if the thickened antennae have been developed from a form like *capensis* with normal sized antennae, why should not also the quadrangular 4th

side-plate have been developed from the more normal *capensis* shape. The question must for the present remain undecided. Further evidence is needed, especially analogous evidence from the Gammarids of other parts of the world. At any rate the present evidence, as far as it goes, supports the warning given above under (*a*), that the quadrangular 4th side-plate *may* be a secondary acquirement and *not* an ancestral feature.

(*c*) A further tendency, not very well marked except in one species, is towards the development of a secondary sexual character on the 1st peraeopod. In the ♂ of *auricularius* the 5th joint is quite abnormally shaped (Barnard **5,** pl. xxvii, fig. 27, and p. 169 *supra*). In *granulicornis* the 4th joint is distinctly widened distally, so that the 5th is very abruptly narrower, giving the species a distinctive appearance.

Secondary sexual characters on the 1st peraeopods are quite unknown among the other species of *Gammarus*, in fact amongst the whole *Gammaridea*, though they are known on the 2nd peraeopod (e.g. the Phliantid *Temnophlias capensis* Brnrd.).

Taking into consideration the above points in conjunction with the topographical evidence set out below, the most plausible conclusion is that *G. nigroculus* represents an ancestral form which was once widely distributed over the whole of the south-west districts. Adverse meteorological conditions have, so to speak, pushed it off the tops of the ranges and out of the old mature valleys down into the youthful streams.

Offshoots, however, have been left behind which by changed habits have been able to meet these adverse conditions, and in course of time have developed certain distinctive characters. They have lost the eye-pigment, and apparently a secondary simplification of the 4th side-plate has set in.

IV. General Considerations.

A. *The Distribution of the Freshwater Crustacea of South Africa in Relation to the Topography.*

The observations on this aspect have all been made in the Cape Province. I have had no opportunity of studying the topography of the habitat of *Eucrangonyx robertsi* in the Transvaal; and the few localities which I have visited in Natal have proved unsuitable for freshwater Isopods and Amphipods (see Causes of Restriction).

It will be best to discuss the various localities separately, taking Table Mountain first. (See Map, Pl. V, and also Barnard, **6.**)

Table Mountain and the Cape Peninsula (Map, A).—This isolated outlier of Table Mountain Sandstone reaches a height of 3500 feet at its northern escarpment, whence it stretches away southwards as an almost unbroken ridge, diminishing in height to the Cape Point.

The perennial streams are mostly in the northern part, as would be expected, seeing that here is the greater mass of rock to form a reservoir for ground water. Moreover, the highest portions receive during the summer months a considerable amount of moisture condensed from the south-east mists (see Meteorology).

It is this northern part—Table Mountain proper—which is most interesting for our present purpose, harbouring as it does *Phreatoicus* and four species of *Gammarus*, and presenting certain topographic features which appear to provide very valuable clues to the history of the Crustacean fauna.

From the " Front Table " southwards there is a series of valleys running in a general west to east direction, i.e. roughly at right angles to the axis of the Peninsula : thus the Waai Vlei Valley, the valley between Kasteels Poort and Skeleton Gorge, in which are situated the Municipal Reservoirs, a valley north of Groote Kop and another south of the same peak, and several others. All these valleys are comparatively broad and flat and drained by a sluggish, more or less meandering stream, presenting all the appearances of mature valleys.

But cutting through these valleys is a stream of a very different character, rapid, with steep uneven gradient and deeply entrenched in a high-walled precipitous gorge. This, the Disa (Palmiet) stream, is a typical youthful stream which has been following up a fault or line of weakness, cutting right back into the heart of the mountain, and capturing the drainage waters of all the above-mentioned older valleys.

The streams in the gorges on the west, north, and east escarpments are, of course, also youthful mountain streams engaged in the demolition of Table Mountain.

When the survey of Table Mountain was completed and the distribution of the various species of Crustacea charted, the most striking feature was the separation of the " black-eyed " *G. nigroculus* from all the other species of *Gammarus* and *Phreatoicus*.

G. nigroculus is found on the *lower* slopes at the foot of the northern and eastern escarpments of the main Table and around Devils Peak. It ranges from about 200 feet altitude up to about 1000 feet, and is confined to streamlets and runnels containing perennial *surface* water, only reaching the 1000 feet contour in the larger streamlets like that in the Platteklip Gorge. (Pl. VII, fig. 2.)

Above this height this Platteklip stream, which in winter courses down among boulders in a rocky bed, is in summer non-existent as a *surface* stream. Such also is the case with the Silverstream on the northern escarpment, and the various streams on the eastern (and western) escarpment. In each case the upper limit of this species of *Gammarus* is dependent on the presence of perennial water at the surface. Thus we do not find it

southwards beyond Muizenberg, where the mountains come close to the shore and are much lower, and whence southwards scarcely a perennial stream exists. Nor do we find it on the western slopes of Table Mountain because apparently the granite forming the base of Lions Head and the nek (=col) between that peak and Table Mountain throws out no perennial surface streams and thus acts as a barrier to its dispersal in this direction. Also it is entirely absent from the top of the Table, for although doubtfully recorded from the Table top in my original description (**5**) I have never yet found it there again, so that I am convinced that the label attached to those specimens was erroneous.

The streams on the top of the mountain, however, are the home of *Phreatoicus* and the "blind" species of *Gammarus*. In two of the old valleys, Waai Vlei (Pl. VI, fig. 1) and that at the top of Kasteels Poort, *Phreatoicus* and *G. capensis* and *auricularius* abound.

The first and last are found nowhere else on the mountain, but *G. capensis* is widely distributed over the whole Peninsula. Besides living in streams which flow on the surface throughout the year, it can be found also in certain caves through which run more or less subterranean channels which disappear during the summer months, as e.g. near the head of Fountain Ravine. Since the rock composing the mountain is traversed by innumerable joints and fissures, it would seem that as the level of the telluric water sinks and the surface water disappears the animals work their way down among the crevices. Thus they would be able to survive and make their appearance again when the water rises in the wet season and is thrown out in surface channels.

This species likewise occurs in one or two places in the upper part of the Platteklip stream, but it comes down as low as about 1000 feet, where its range meets that of *nigroculus*.

As we proceed southwards along the Peninsula *capensis* is found at still lower altitudes: on the Muizenberg and Kalk Bay mountains and around Noordhoek from 1500 feet down to 500 feet, and in the extreme south at Buffels Bay at scarcely more than 300 feet.

Thus altitude *per se* is not a factor in the distribution of these animals, only in so far as it affects the level of the telluric water and the perennial nature of the streams.

The only other species, *G. crassicornis*, which is found on the mountain, ekes out its existence as already stated in the merest trickles arising from grotto-like places on the escarpment cliffs of the Table, and, like *capensis*, seems to withdraw during the dry season into the inner recesses of the rock crevices where it finds perennial water.

The important points to notice in regard to the distribution of the Crustacea on Table Mountain are: the occurrence of *Phreatoicus* in the

older mature valleys ; the restricted range of *G. nigroculus* in the *lower* north and north-east slopes of the Table compared with the wide range of *G. capensis* over the whole of the Peninsula.

This relationship between the distribution of the various species and the topography, first observed on Table Mountain, was found to be exhibited even more clearly in certain parts of the Hottentots Holland Mountains, and particular attention was paid to it in all subsequent exploration and collecting.

The Hottentots Holland Mountains (Map, B).—In discussing this range of mountains it will be convenient to divide it into two parts : the northern part from the Sneeuwkop to the Spitzkop, the streams of which running eastwards drain into the Zonder End and Palmiet Rivers ; and the part south of the Spitzkop which forms together with the Kogelberg the catchment basin of the Steenbras River. The whole range like Table Mountain is composed of Table Mountain Sandstone.

The first portion is the highest, rising to 4500 feet (Landrost Kop) and 5100 feet (Sneeuwkop). The strata dip gently to the south-east, forming a steep and precipitous escarpment on the west.

The various peaks are more or less isolated, and between them are the remains of several ancient plateaux or broad flat valleys (Pl. VIII, fig. 2). The present streams on the dip slope arise in or near these valleys, but after a short distance enter on precipitous, deeply entrenched courses, which indicate their youthful and rejuvenated character.

Where the stream arises in the ancient valley (e.g. between Landrost Kop and Valleiberg) a waterfall is interposed between the youthful portion and the meandering headwaters in the old valley. To the north of Landrost Kop is an example of the youthful stream having cut right back through the old valley, the meandering stream from which now enters the main stream as a side tributary over a cliff.

The new and the old valleys in this portion of the range are thus perfectly separated by barriers which are insurmountable by animals of the type under discussion.

Further, there are in places springs or runnels issuing from grotto-like cavities on the sides of the peaks, and running a short distance above ground and then disappearing. They are in all cases well above the present youthful streams.

In this district three species of *Gammarus* have been found. In all the tributaries of the youthful streams *nigroculus* occurs and *no other* species. "Blind" species, on the other hand, are found in the meandering streams of the old valleys, where they are associated with *Phreatoicus*, and in the grottos on the hillsides ; *aurantius* occurs in the former habitat, *seticornis* in the latter.

Farther to the south, in the neighbourhood of the Spitzkop, the mountains decrease in height, the Spitzkop itself (4000 feet) standing up well above the general crest of the range. At its base on the south is a rather narrow plateau (2000 feet altitude) from which arise the Steenbras River flowing south-east, and two other streams flowing north-east and later joining the Palmiet River.

The break between the youthful and mature portions of the stream is here not so distinct as farther north, which is due apparently to the lesser amount of uplift suffered by the southern part of the range.

Thus while two " blind " species of *Gammarus* (*spinicornis* and *granulicornis*) together with *Phreatoicus* were found in the streams flowing off the plateau above mentioned and some little distance below, it was not surprising to find the black-eyed *nigroculus* penetrating into the domain of the former. *G. nigroculus* does not, however, appear on the actual plateau, where *Phreatoicus* and the other Gammarids remain the sole Crustacean inhabitants.

The Steenbras Basin (Map, C).—The watershed between the basins of the Palmiet and Steenbras Rivers is very low. The latter river flows through a shallow strike valley, 3–4 miles wide, bounded on the north-west by the southernmost part of the Hottentots Holland Mountains, and on the south and south-east by the Kogelberg and its foothills. (Pl. VIII, fig. 1.)

It is clear that this valley once formed part of the Palmiet basin, and that a reversal of drainage has occurred. Both the Kogelberg stream and the Steenbras were originally tributaries of the Palmiet, but have been tapped and caused to flow in the opposite direction by the cutting back along a line of weakness or fault of an escarpment stream.

The upper part of this basin is intersected by numerous runnels, many of which are dry in summer, and portions of it are marshy throughout the year. *G. spinicornis* and *granulicornis* are here abundant, usually living together, and in association with *Phreatoicus*. In the upper reaches of the main source of the Steenbras both *nigroculus* and *seticornis* occur; near the mouth of the river in the little side streamlets *seticornis* is again found. Further, this species is also found on the west side of the Hottentots Holland Mountains on the slopes below Sir Lowry's Pass in streamlets feeding the Lourens River.

This last occurrence is clearly due to the capture of one of the dip-slope streams by a more rapidly eroding escarpment one. The watershed is being displaced eastwards, and the Crustacea which are now living in the basins on the east side will in time be transferred to the basin of the Lourens River on the west side, provided they survive the passage down the rapidly flowing escarpment streams, and find suitable places of refuge in the side runnels. Several actual stages of this process can be seen in parts of the

range about the Spitzkop, and in one place there is a pool containing *Phreatoicus* and Gammarids on the crest of the range a few yards to the west of the actual watershed and within a few yards of the start of the precipitous escarpment stream.

The Kogelberg (4000 feet) with its foothills lies to the south-east of the Steenbras Valley. It is of the "hogsback" type of structure with intervening strike valleys. The Kogelberg stream which joins the Steenbras has cut through two of the ridges, and in one place forms a sharp hairpin bend. Erosion has kept pace with the uplift. The Crustacean fauna includes a "blind" Gammarid, *kogelensis*, a variety of *Phreatoicus capensis*, and the interesting freshwater Jaerid described above. All three are found together in the headwaters of the stream where the ground is boggy, before the stream has got rapid and precipitous. The black-eyed *G. nigroculus* seems to be absent from the neighbourhood of the Kogelberg, though I have not yet examined its southerly or south-easterly slopes, which are drained by some of the headwaters of the Palmiet River.

In regarding the whole of this district the striking point is this: wherever the older valleys are well and distinctly separated from the youthful valleys by waterfall barriers impassable to Crustacea, there also we find a separation of the "blind" Gammarids and *Phreatoicus* on the one hand from the black-eyed *G. nigroculus* on the other hand. This is more particularly noticeable in the northern part of the range.

Where the topographical barrier has been broken down, e.g. in the southern portion of the range near the Spitzkop, there we find a mingling, though seemingly only incipient, of the two groups. (See further, Barnard, **6**.)

Stellenbosch and French Hoek Mountains (Map, D).—Continuing along the Hottentots Holland Range northwards we pass insensibly into the Stellenbosch and French Hoek Mountains. Throughout this district, wherever suitable habitats occur, *G. nigroculus* is to be found. Thus, at the head of the Jonkers Hoek stream, a tributary of the Eerste River; on the southern slopes of the Dwaars Berg up to the foot of the Victoria Peak at 4000 feet altitude in the headwaters of a tributary of the Zonder End River; in the stream on the eastern side of French Hoek Pass (also a tributary of the Zonder End River); and in the Waterfall Kloof on the north side of Drakenstein Peak.

In each case the stream is a youthful one which has cut right back into the mountains.

No "blind" Gammarids have been found in association with *nigroculus*.

Wellington Mountains (Map, E).—These mountains are a continuation of the preceding ranges. They have been considerably tilted up and cut into deep valleys and gorges. A shale band at a high level on some of the

peaks causes more or less level stretches which are well watered in the wet season, but dry up during the summer.

The Witte River Valley is a wide and open valley watered by a perennial stream. Contrary to expectation, no *Phreatoicus* or "blind" Gammarids have been found here, though *nigroculus* is present in some of the side streamlets.

Tulbagh, the Winterhoek Mountains, and the Witzenberg Range (Map, F). —This area lies to the north of the Wellington Mountains.

The Tulbagh Valley drains into the Klein Berg River, and is separated on the north by a high nek, 4000 feet altitude, from the headwaters of the Twenty-four Streams. Both rivers eventually meet.

On both sides of this nek *G. nigroculus* is found. But only in one spot on the north side, in the Sneeuwgat Valley, was a "blind" species discovered. This was *G. tulbaghensis*, and it was found in a marshy place on the hillside considerably above the present main stream.

The Winterhoeks and the Witzenberg Range are formed of strongly tilted strata, and there is a noticeable absence of high-level plateaux and broad valleys, apparently for reasons which will be adduced below. (See Causes of Restriction).

The Cedarbergen (Map, G).—The Cedarbergen or Clanwilliam Mountains lie still further to the north. The folded belt is here beginning to die out, and the mountains are composed of more or less horizontally disposed strata, though they have been subjected to very strong denudation.

Vlaktes and mature valleys at high levels are common, but owing to the absence of moisture-laden winds during the summer months they dry up completely. In some of the less precipitous parts of the youthful streams *G. nigroculus* occurs.

No investigations have been made north of this area.

Ceres (Map, H).—Another district which lies within the region of the strongly tilted and contorted Table Mountain Sandstone strata is Ceres. The mountains in the actual neighbourhood of Ceres I have not yet examined.

East of the town is a broad expanse of undulating country formed by the Bokkeveld beds, which overlie the Table Mountain Sandstone and have also, though to a less extent, been folded. The Table Mountain Sandstone formation forms the mountains to the south, the Matroosberg, and Hex River Mountains, and also crops out in places as inliers in the Bokkeveld country, where it throws out perennial springs.

In this district only *G. nigroculus* was found. It occurred in a stream on the farm "De Vlakte," which flows down the Valschgats Kloof into the Hex River, eventually joining the Breede River. It was also found on the farm "Uitkomst," where a perennial spring arises from an inlier of Table Mountain Sandstone.

All the surrounding streams on the Bokkeveld formation dry up completely during the summer. They lack in consequence an abundance of vegetation on the banks and the accumulation of vegetable debris, and thus offer, apart from the lack of water, no suitable habitats for Gammarids or *Phreatoicus*.

Nor were suitable habitats for these animals found in the mountains around the Matroosberg, for the same reason probably as in the Tulbagh district.

Farther to the north, beyond the outcrop of the Bokkeveld beds, are the more or less horizontal beds of the Witteberg series. These beds are essentially similar to the Table Mountain Sandstone as regards perennial streams and resistance to weathering. Up to the present I have had an opportunity of exploring only a very small area in the neighbourhood of the farm "Welgemoed," west of Hottentots Kloof. No Crustacea were discovered.

The Zonder End Mountains (Map, I).—This range runs from the mountains around French Hoek nearly as far as Swellendam, south of and nearly parallel with the Langebergen. It is a large anticline of Table Mountain Sandstone, with an east-west axis, arising out of a Bokkeveld plain. Its highest peak, the Zonder End Peak, reaches 5460 feet, and the greater part of the crest is about 4000 feet.

A great deal of the southern arm of the fold has been completely denuded away, but the arch still remains intact on both north and south sides at the Zonder End Peak. On the southern slopes of this peak there is at 3600 feet altitude a small boggy valley, which evidently once extended much farther westwards. It is drained by a small consequent stream, which after leaving the valley flows over a rocky bed with a few minor waterfalls, into the River Zonder End. Here are found *Phreatoicus* and *G. spinicornis*.

The main drainage of the upper parts of the southern slopes is carried by the Olifants Bosch River. This river in its lower course is a consequent stream flowing southwards, but in its upper part becomes a subsequent stream flowing eastwards along the strike. There are no marked waterfalls except in its lower portion.

In this stream the black-eyed *G. nigroculus* is found up to about 3600 feet. Its place is then taken by a "blind" species, *spinicornis*, associated with *Phreatoicus*, both of which continue right up on to the crest of the range (4500 feet), on the west of the summit of the Zonder End Peak, and also just over the crest on to the north side of the watershed. The ground here is boggy and peaty, and is evidently moist throughout the year. Probably there are few days in the year, even in the dry season, when the surface water completely disappears, because the range is fully exposed to the south-east mists.

The Langebergen: Montagu (Map, J).—The Langebergen is a range of very highly tilted Table Mountain Sandstone strata with an east-west strike, extending eastwards from the Hex River Mountains. I have examined a limited portion of this range in the neighbourhood of Montagu. On both sides of the Kogmans Kloof there is a total absence of high-level vlaktes and bogs. This end of the range is outside the area of the south-east mists.

No Crustacea of the groups in question were discovered.

The Langebergen: Swellendam (Map, K).—Farther to the south-east, however, in the neighbourhood of Swellendam and the Tradouw Pass, the range comes within the area of the south-east mists, and conditions very similar to those in the Zonder End Mountains are found. There are several high-level bogs and marshes inhabited by *Phreatoicus* and *Gammarus*.

Summary of the South-West Districts.—Although this preliminary survey has touched many localities scattered over a moderately wide area, yet it is obvious that many more localities remain to be searched before we can state with certainty the limits of distribution of these Crustacea in the south-west mountains.

We may, however, summarise the above topographical investigations and map out roughly the distribution of the various forms.

In localities to the south and south-west of the more highly folded ranges broad mature valleys and vlaktes still remain, though considerably reduced by denudation and stream erosion. In such habitats, *and nowhere else*, does *Phreatoicus* live. Altitude *per se* is not a factor, as *Phreatoicus* has been found at various heights: 1500 to 4500 feet.

In similar habitats, and in springs and runnels high up in the mountains, are found several species of *Gammarus*, all characterised by the absence of black ocular pigment, and (in most cases) small size. Many of these runnels dry up in the summer time, and the animals must evidently withdraw far into the crevices of the rocks where a certain modicum of moisture remains throughout the dry months.

These species of *Gammarus* collectively are found over a wider area than *Phreatoicus*.

An even wider area is occupied by the single black-eyed species *G. nigroculus*. Yet the habitats of this species do not coincide with, and only at one or two places touch, the habitats of *Phreatoicus* and the other Gammarids. This species is only found in the smaller streamlets in youthful valleys where there is perennial surface water.

B. *The Habitats of the Australasian Freshwater Crustacea in Relation to the Topography and Geology.*

1. *Phreatoicidae.*—At the outset we are met with the difficulty that observations definitely from this point of view have not been taken, but some indications can be derived from the published accounts of Helms and Chilton for *P. australis*, of Sayce and Chilton for *P. shephardi*, and of Smith for the Tasmanian species.

Helms, the original discoverer of *P. australis*, has given a concise account of the Kosciusko pleateau where the species occurs. He states (Pr. Linn. Soc., N.S.W., viii, p. 349, map) that there are extensive flats obviously formed by glaciers, with terminal moraines blocking the drainage and causing bogs. Further, Chilton (**11**, p. 149) quotes Helms as follows: "The creek runs here through a, in damp weather, boggy flat, and at the time (early March 1889) was slowly trickling along forming puddles here and there," and continues, "the locality is nearly at the top of a branch of the leading plateau that extends, with various interruptions, towards the Ram's Head, Mount Townsend, and Mount Kosciusko, the highest points of the range, and is only about half or three-quarter mile from the rise which forms the watershed between the river basins on the north and south. This rise is only about 30 or 40 feet higher than the place at which the animals were found."

Although I have seen no contour map of this district, nevertheless I think one is justified, if Süssmilch's statement * applies here also, in presuming that below these broad valleys there are waterfalls, or at least the river becomes obviously a rejuvenated stream, rapid and precipitous.

But clearer evidence confronts us in regard to *P. shephardi* from Barrington Tops in the New England Plateau. Chilton (**13**) states that "the broad shallow valleys of the highest part of the plateau originate in large swamps that are almost peat bogs." Further, Andrews (**2**, p. 509) describes how as the eastern rivers approach the plateau the valley walls close in and the streams end in waterfalls. "Above the falls the stream-paths are confined for short distances to narrow and steeply inclined valleys, but these features pass up-stream quickly into shallow valleys of decided width and gentle grade. Such a type is often ascertained to be enclosed within another shallow, but broader, valley . . . thus presenting the appearance of a peneplain dissected to the stage of maturity. Sometimes these mature

* "The cycle of erosion initiated by the Kosciusko uplift is still in progress. . . . The streams, rejuvenated by the uplift, held their courses against the rising land, and have, for the most part, entrenched themselves in their old channels . . . the central parts of the tablelands being still more or less intact" (Süssmilch, An Introduction to the Geology of New South Wales, 2nd ed., 1914, p. 216).

valleys are of such breadth as to suggest the excavation of one peneplain surface out of another. Above these, again, rise the many residual plateaux . . . consisting of the more resistant granites."

We could desire no clearer description of the topography of this locality of *P. shephardi*. Of its habitat in Victoria we have only the short statement of Sayce (**30**) that the "geological formation is a small granite area, surrounded by a wide expanse of Upper Silurian."

With this evidence we feel fairly safe in drawing attention to the similarity in the habitats of these two Australian species and the Cape species. Their occurrence in the higher mature portions of the river systems indicates their long occupation of these regions, and justifies us in terming them relicts from the time of a former more extensive peneplain. From what we know of their present-day habitats it is impossible for them to have reached these plateaux *since* the tertiary uplift, for the streams end in waterfalls where the animals cannot live.

Tasmania offers evidence of how *P. australis*, still living in several localities at considerable altitudes, has been let down in two other localities to sea-level owing to the subsidence of the south-east portion of the island (Smith, **33**), the estuary of the Derwent being a fiord or sunken valley (*cf.* south-west corner of New Zealand).

We must now notice the localities of the other forms. *P. australis* and *shephardi* are the modern representatives of the generalised stirps (see p. 161). The other forms, namely *Phreatoicopsis* and *Phreatoicoides*, are specialised in certain directions and have adopted semi-terrestrial burrowing habits.

Neither of these forms is found within the area of the uplifted Palaeozoic rocks, but instead they occupy low-lying stations on the freshwater Jurassic or the marine Tertiary beds of Southern Victoria.

Thus the morphological characters which induce us to regard these species as recent derivatives from the older stirps are supported by these geographical facts. For it is evident that these species have only occupied their present haunts since Tertiary, nay, even late Tertiary, times, the present outcrop of the Jurassic beds having been in all probability covered by the Tertiaries.

Contrasted herewith is the occurrence of a third specialised burrowing form, *Hypsimetopus*, in the Western Palaeozoic highlands of Tasmania. This, however, need not vitiate the conclusions drawn from the Victorian forms, for it can be interpreted as showing that specialised forms may arise from the stirps in its ancient locality and be ready to invade new lands when such are elevated above the sea and become habitable.

In New Zealand the two species, *P. typicus* and *assimilis*, are blind and subterranean, and therefore have little bearing on the questions relating

to topography. *P. kirki* and its variety *dunedinensis* are also blind and pale in colour, and evidently were once subterranean in habit, though found at the present day in surface streams.

2. *Gammaridae.*—The relation between the habitats and the topography in the case of the Australasian Gammarids needs investigation even more than in the case of the Phreatoicids, and offers a fine field for Australian zoologists. Chilton (**12**) alone has discussed the question, and his discussion centres mainly round the origin of the subterranean fauna.

C. *Meteorology.*

Under this heading there are two points to consider:

(1) The rainfall and precipitation of moisture.

(2) The temperature of the water.

1. It is clear that in discussing meteorological conditions as they affect aquatic animals, the bare determination of the amount of annual rainfall will not teach us much. We want to know the distribution of that rainfall throughout the year to determine the driest month or months, and, most important of all, the *reliability* of the rainfall in the dry season. For an extra severe drought might lead to a widespread killing off of the animals, which in some localities might mean their extermination beyond the possibility of rehabilitation. Such indeed might well happen with *Phreatoicus* in any one of the localities, because it occupies positions which are quite isolated from one another.

The required statistics, however, are not easy to obtain. To the circumstance that Capetown draws its water supply from reservoirs on Table Mountain is due the installation of several rain gauges actually on the mountain. Two or three of these are quite close to the *Phreatoicus* localities, viz., Waai Kopje, St. Michael's Mountain, and Disa Head (Ranger's Hut). The records from these stations are very valuable for our present purpose, for they are the only *mouhtain* stations in the whole of the south-west area under discussion. In the case of the other haunts of *Phreatoicus* we can only argue by analogy.

On an ordinary rainfall map the whole area in which aquatic Crustacea (of the two groups in question) have been found lies within the 25-inch isohyet. But the small-scale generalised map takes no account of mountain stations and thus Table Mountain is not distinguished from the surrounding low country, yet the rainfall in the two cases is utterly different, as may be seen from the following table:—

	I. Cape Town (Royal Observatory). 40 ft. alt.	II. Table Mountain (Waai Kopje). 3100 ft. alt.	
April . .	1·84	5·23	
May . .	3·25	9·06	
June . .	3·26	10·40	
July . .	3·06	8·90	
August . .	3·08	8·39	
September .	2·27	5·82	
October . .	1·60	5·31	
November .	0·86	3·29	*
December .	0·71	3·28	3·16
January .	0·37	2·26	1·85
February .	0·44	1·83	1·75
March . .	0·86	3·06	2·91
Yearly Mean .	25·01	66·83	

Figures taken from Stewart (**36**) for the years 1882–1911 inclusive. Those under (*) are from data supplied by the Meteorological Office, Pretoria, and cover a period of 37 years, 1882–1918 inclusive.

It will be seen that not only is there a considerably greater deposition of moisture on the top of Table Mountain, but that there is a very fair amount of precipitation during the driest (summer) months, which is the critical period for these animals. This is due to the "Table Cloth," the bank of mist which is formed when the South East Trades blow.

A few years ago some experiments were conducted to determine the amount of moisture deposited from these south-east clouds, as it was thought that considerably more was deposited than was recorded by the ordinary rain gauges (Marloth, **21** and **22**). Although Marloth's actual figures have been criticised, there is no doubt that a very large amount of moisture, over and above that recorded by the ordinary methods, is deposited on the vegetation and finds its way to the soil below, and that his general description of the climatic conditions is correct.

Marloth set out "to ascertain more exactly the climatic conditions under which the plants on the mountain existed" and he found that: "Their summer is not dry. Their climate is that of a swamp—a permanent swamp in winter, a periodical swamp in summer, which dries up during a long spell of fine weather, but becomes soaking wet during the days of the south-east cloud. These results explain why such luxuriant and thickly set vegetation prevails on the upper parts of our mountains . . . and why there are little lakes, even late in summer, on the top of Table Mountain. . . ." (**21,** p. 408).

The amount deposited may not always be enough to keep the streams flowing continuously, but it is certainly enough to keep the ground *moist and cool* beneath the banks of the stream where there is a matted mass of vegetation. (See Aestivation.)

Thus the mist clouds formed by these south-east Trades may be said to be one of the essential factors governing the existence of *Phreatoicus* and, to a lesser extent, *Gammarus*.

The possibility, however, of a long spell of fine weather is not excluded, and therefore it is necessary to examine the reliability of the rainfall for the summer months.

The reliability is usually expressed by the average deviation from the mean (in per cent.), but there is also the relative *frequency of a deficiency* to be considered. From data supplied by the Meteorological Office, Pretoria, I have calculated these two factors for the Waai Kopje on Table Mountain :

		Average Deviation from Mean.		Frequency of Deviation.	
Waai Kopje, Table Mountain, 3100 ft. alt.	December	50·9	Average 47·2	51·3	Average 54·8
	January	51·3		59·4	
	February	45·4		56·7	
	March	41·5		56·7	

Both factors, it will be observed, are high. But that this is no unusual occurrence at mountain stations will be seen by a comparison with similar tables for the three drier months at two Australian stations, one quite close to the haunt of *Phreatoicus australis*, the other situate on the same

		Average Deviation from Mean.	Frequency of Deviation.
Mt. Kosciusko, N.S. Wales, lat. 36° S. 5018 ft. alt.	February	46·9	66
	April	50·4	44
	November	53·7	50
	Average	50·3	53·3
Armidale, N.S. Wales, lat. 30° S., 3333 ft. alt.	May	51·7	56·3
	July	43·5	58·1
	August	40·0	62·5
	Average	45·0	58·9

plateau as the locality of *P. shephardi*, though considerably farther north.*

Clearly, therefore, the conditions for these animals cannot be too favourable as regards the deposition of moisture. With a deficiency of rain (for the months quoted) in more than fifty years out of a century, and that deficiency measuring on an average nearly, or even over, 50 per cent. of the mean, it is not surprising that the *Phreatoicids* have developed the power of aestivating in damp earth and the *Gammarids* seek refuge in the deep cracks and crevices of the rocks where there is perennial water.

In other respects, of course, the climate of Mount Kosciusko on the New England plateau must not be compared with that of Table Mountain, and the relation between the climate and the habits of *P. australis* and *shephardi* must be worked out on the spot by someone familiar with the climate of those localities.

The other factor which may be of importance is the temperature of the water in which the animals live.

It is well known that Crustacea are not adversely influenced by the *coldness* of the water so much as its *warmth*. Exceptions are, of course, known as e.g. *Apus*, which needs a relatively high temperature for its development; and a few Crustacea which have become accustomed to live in hot springs.

Phreatoicus is no exception to the general rule. Helms found *P. australis* on Mount Kosciusko under stones which were frozen hard, and Chilton (**11**) states that "for six months in the year the place is covered with snow and the ground itself is probably frozen." So that it is evidently more important to ascertain the maximum temperature at which these animals can exist.

On Table Mountain I have made a series of observations, extending over several years, on the water temperature. The resultant curve is shown on the growth chart (text-fig. 2). It does not purport to be perfectly accurate to a degree; nor does it necessarily hold good for streams in the Hottentots Holland Mountains or other localities, where I have had no opportunity of making continuous or even frequent observations.

It seems to show, however, in a general way that the animals are moderately eurythermal. Probably they would be found capable of withstanding a greater amount of cold than that to which they are naturally exposed, if suitable experiments were tried. But it is doubtful if they could exist under much warmer conditions.

The maximum temperature I have recorded is 68° F. (=20° C.).

I also attempted to ascertain the temperature to which the animals are exposed when they are aestivating, but the results were too unequal to

* Figures calculated from data kindly supplied by Dr. Griffith Taylor, formerly of the Australian Commonwealth Meteorological Bureau.

have any value. It is well known, however, that peat is a bad conductor of heat.

Having found that the existence of *Phreatoicus* is dependent on the deposition of a certain amount of moisture during the late summer months, I endeavoured to trace the limits of effective deposition of moisture from the south-east clouds in the south-west mountains.

By personal observation and inquiries amongst mountaineering friends who are well acquainted with these districts, I find that to the north of a line running roughly west to east through Table Mountain, French Hoek, and the Zonder End and Swellendam Mountains, the south-east mists do not occur, or are so diminished in intensity and duration that from the present point of view the amount of moisture deposited is negligible.

Although there are several localities not far to the north of this line apparently suitable in other respects for *Phreatoicus*, they become so excessively dry as to be uninhabitable by the animals even in an aestivating condition.

Thus the northerly limit of effective deposition by the south-east clouds coincides approximately with the northerly limit of the distribution of *Phreatoicus*.

D. *The Present-day Restriction of the* Phreatoicidae *to certain limited Regions.*

The widespread but discontinuous geographical distribution of the *Phreatoicidae* would have indicated, without any palaeontological evidence, that the family is a very ancient one, and that its present-day haunts are of the nature of asylums. As Suess says (Antlitz, 4, p. 671): "Asylums reveal themselves as ancient lands both by their structure and by the fauna of their rivers."

It is seen that those species of the tribe, which are morphologically nearest the ancestral stirps, occupy the remnants of ancient peneplains composed of palaeozoic or older rocks which have been raised out of reach of marine transgressions since early mesozoic times, and which are considered to have formed part of the Gondwanaland continent.

Since the Triassic fossil species, *wianamattensis*, presents us with, as far as can be determined, all the peculiarities characterising the tribe (Calman **10**), we can legitimately suppose the tribe arose in permo-carboniferous or earlier times. We can scarcely avoid connecting it with the then widely prevailing glacial conditions and the *Glossopteris* flora.

The "break up" (see further p. 209) of the Gondwanaland continent divided the tribe into an African group (*capensis*) and an Australian (*australis-shephardi*). From the ancestors of the latter group several

derivative forms have arisen in response apparently to favourable conditions. Up to the present no derivatives of the African group have been discovered.

A branch of the original stirps also managed in some manner to reach New Zealand, where it has developed subterranean habits and, by secondary adaptation, one species in surface waters.

But besides marine transgressions we must look for some other cause which has restricted the animals to the circumscribed areas on the respective continents they now occupy. Two causes seem to have been operative in this respect: extensive volcanic activity and glaciation. In New Zealand the extent and duration of the marine transgressions alone would have been sufficient to lead us, had we not known of their actual occurrence, to feel almost certain *a priori* that no Phreatoicids would ever be found in that country.

(*a*) *Causes of Extinction in South Africa.*—In this country the destructive influence of the volcanic outburst was probably not so great as elsewhere, for though the Drakensberg lavas formerly covered an enormous area to the north of their present occurrence, they are not considered to have spread over the whole of the southern or western folded belts, and thus it is possible for *Phreatoicus* to have escaped.

As there has been no Pleistocene glacial period as in south-east Australia it is necessary to find some further cause or causes leading to the restriction of *Phreatoicus* to certain spots in a comparatively small area in the extreme south-west. The following explanation seems to be feasible.

Phreatoicus is nowadays confined to certain spots on the Table Mountain Sandstone mainly *outside* the folded belts, i.e. south and south-west of Worcester. In this direction these folds die out. The strata of Table Mountain are horizontal, and those in the Hottentots Holland and Zonder End Mountains dip at a comparatively slight angle. But if we trace the mountains through French Hoek to the Witzenbergen and Hex River Mountains we find that the earth movements have been more intense, the strata have been considerably more tilted, and in consequence are much more fractured.

For this reason, and owing to the fact that they reach a greater altitude, these mountains have been more exposed to the action of denuding agents: a greater rainfall in winter, a lesser deposition of moisture in summer, and a consequent meagreness of the protective covering of vegetation. In these parts of the mountains therefore it is not surprising that all traces of old high-level plateaux have been denuded away. No marshy valleys or slowly flowing streams, such as are requisite for the existence of *Phreatoicus*, are to be found. The scarcity or complete absence of "blind" Gammarids is also to be ascribed to the same cause; while the black-

eyed species is only to be found in these districts in the small side runnels not exposed to the full force of winter torrents.

Throughout the whole of the folded belts where extreme tilting and fracturing has taken place the same factors will probably be found to have been operative in reducing and abolishing the areas suitable for *Phreatoicus*.

Farther south in the Hottentots Holland Mountains the *Phreatoicus* area is being relentlessly narrowed down by the action of the rejuvenated and the escarpment streams, a process of which a particular example has been given above (p. 193).

But while nowadays *Phreatoicus* and the Gammarids find suitable habitats on the Table Mountain Sandstone it is safe to say that they have not always lived on this formation. Therefore some of the other geological formations, so far as localities situated on them have been visited, may be reviewed as to their potentialities for supporting these Crustacea.

Overlying the Table Mountain Sandstone are the Bokkeveld beds, a series of sandstones and shales, which are exposed over a wide area east of Ceres and around Caledon. These rocks are comparatively soft and unresisting, and form stretches of rolling country.

In summer the soil becomes baked and parched and all the streams run absolutely dry. Such a country is obviously unfit for these Crustacea, and supposing they were once existing on the overlying strata, when once denudation had brought them down to the Bokkeveld their days were numbered. Unless indeed we admit that a more pluvial climate prevailed over these districts at the time.

Some such explanation seems necessary in order to account for the presence of a colony of *G. nigroculus* in a stream arising from an inlier of Table Mountain Sandstone (on the farm "Uitkomst" in the Ceres district; *supra*, p. 195), completely surrounded by Bokkeveld beds. For before the stream had cut back and tapped the perennial spring thrown out by the Table Mountain Sandstone, it must have flowed for a long period over the Bokkeveld, which under the present prevailing dry conditions would have been fatal to the continuance of the Crustacea.

There is another possible cause of the absence of Crustacea from the streams on the Bokkeveld formation, namely, the chemical composition of the water. Whereas the waters draining from the Table Mountain Sandstone are exceedingly pure, those from the Bokkeveld beds (as also the Dwyka and the Cretaceous Uitenhage beds) are markedly saline (Juritz. **19**, p. 756). The chemical composition of the water may, of course, have no effect whatever on these Crustacea. The water in the limestone caves at Makapan appears to be by no means prejudicial to *Eucrangonyx*. I am not aware that any experiments have been made to test the matter, or whether the distribution of the European *G. pulex* and *Asellus aquaticus*

has been worked out in regard to the underlying geological formation and the chemical composition of the water. This might possibly prove an interesting study.

Above the Bokkeveld beds are the Witteberg beds, hard sandstones much resembling the Table Mountain Sandstone, and forming nearly horizontal plateaux capping the Bokkeveld beds. This formation has not yet been explored.

We see how at the present day the Bokkeveld country forms a complete barrier to the dispersal of these Crustacea, and therefore it seems that if they had to cross these beds to reach their present habitats the climate must have been considerably more pluvial and probably cooler.

In this connection it is interesting to refer to the extinction of *Lepidurus* in South Africa. Fossil remains (together with Estheriids) are found in the Cave Sandstone of the Karroo series associated with insect remains, though up to the present they are known only from a very thin band (Haughton, Ann. S. Afr. Mus., xii, p. 328, 1924). To-day *Lepidurus* has been entirely replaced by *Apus*.

Brauer (**9**, pp. 586 *sqq.*) made some observations on the habitats of *Lepidurus* and *Apus*, and some experiments in hatching their ova. He found that the ova of *Lepidurus* were unable to develop if they were desiccated, whereas in the case of *Apus* desiccation was a necessary condition, without which the eggs did not hatch. From this it seems clear why *Lepidurus* has a more boreal or polar distribution than *Apus*, and is confined to pools and bogs on moors where the peaty bottom never completely dries up.

This explanation is borne out by comparing the distribution of the two genera in Australasia, where we find *Lepidurus* occupying New Zealand, Tasmania, and the coastal parts, especially the south-east of Australia, i.e. the moister and cooler parts, while *Apus* appears in the more central parts of Australia, which are exposed to drought.

There is still one more possible cause of extinction, one which is more biological in character than the others.

Methuen (**23**, p. 961), in discussing the presence of *Eucrangonyx* in the Makapan caves, refers to Huxley's theory of the extermination of the crayfishes by the freshwater crabs and prawns. He thinks it possible that these Decapods have been responsible also for the complete disappearance of freshwater Isopods and Amphipods in South Africa, excepting *Eucrangonyx*, which was at that time the only recorded species of these groups. In fact, Methuen makes the definite assertion that the crabs *do* feed on the Amphipods, without however adducing any direct evidence on the point (**24**, p. 949).

It is of course possible, indeed even probable, that crabs do feed on Amphipods, but until we have positive evidence we cannot give this as

a reason for the absence of the latter in situations frequented by former. So far as I am aware no direct observations have been made to ascertain the food of freshwater crabs, in particular the South African species.

With a view to obtaining some evidence on this point I have collected at various times of year some 50 specimens of *Potamonautes perlatus* from a small stream where they live together with Gammarids (*G. nigroculus*). The association is a very close one, for not only are the two animals found in the same stream but in the same clumps of vegetation and debris and in the same crevices of the rocks.

The examination of the stomach contents of these specimens gave no support to the supposition that the crabs feed on the Gammarids. In every case the stomach was found full of *vegetable* matter, the only particles of a chitinous nature being without any possibility of doubt referable to the body rings of a Myriopod (*Julus*), which is frequently found drowned or half dead on the banks of the stream.

This does not of course preclude the possibility that Gammarids are occasionally devoured when the crabs are able to catch so nimble a prey. But when this does not happen in a habitat in which the two animals are living in the closest association we can scarcely regard the crab as a factor in the extermination of the Gammarids.

Certain localities in Natal, where the Table Mountain Sandstone crops out, have also been examined. This region might perhaps *a priori* have been ruled out of account as a possible habitat for *Phreatoicus*, for it was deluged by the Drakensberg lavas, and has since been subjected to powerful and rapid denudation.

All suitable habitats for these animals have disappeared. There are no mature valleys. Where some moderately extensive plateaux are still to be found, as e.g. at Inchanga, they are watered by no perennial streams on account of partly the greater temperature and partly the lithological character of the rock, which is here far more porous than in the South-west Cape district, and thus does not conduce to the retention of the ground-water at a high level.

No aquatic Isopods or Amphipods have yet been found anywhere in Natal.

As regards the south-west region, therefore, it seems that *Phreatoicus* has been extinguished owing to the greater amount of denudation suffered by the mountain ranges in the area of the folded belts. The character of the Bokkeveld beds is such as to preclude the existence of these animals anywhere on its outcrop under present-day meteorological conditions. Similarly the whole of the Karroo may be excluded, for its arid nature is too well known to need discussion.

In Natal we find that the lithological character of the rock and the

meteorological conditions combine to render that region uninhabitable, even supposing the animals were not extinguished by the volcanic eruptions of the Stormberg period.

The Gammarids, with the exception of *Eucrangonyx*, are also confined to the Table Mountain Sandstone, though they have a slightly wider distribution. Though their earlier history may have been different from that of *Phreatoicus* (we have no palaeontological evidence from any part of the world), their later history in South Africa would appear to have been similar.

It is therefore interesting to find *Eucrangonyx* in the Makapan caves, and surface streams in the neighbourhood, in the Transvaal.

These caves are in the Dolomite, a formation of very great age, which retains considerable amounts of water in underground fissures and caves. It might therefore form an excellent asylum for these Crustacea should the surface conditions become impossible. This part of the country, like Natal, was inundated by the Drakensberg lavas, so that the presence of *Eucrangonyx* in the Dolomite caves previous to the eruptions might be doubted. But we have no means of deciding whether *Eucrangonyx* was a later immigrant after the volcanic phase or whether it was part of a previous Gammarid fauna which was widely distributed over Southern Africa in Karroo times, and of which it is the sole survivor in the Transvaal.

Methuen has suggested (**23**, p. 100) a middle or even late Tertiary wide distribution of freshwater Amphipods over South Africa. But in view of our present knowledge, especially of *Phreatoicus* and the associated Gammarids at the Cape and the Australian Rhaetic fossil, we must put the date of this distribution much earlier. The whole point is whether we put it *before or after* the Drakensberg lava-flows. The probabilities seem to point to the earlier date.

From the standpoint we have now reached it is tempting to proceed farther, and from a consideration of the geology of South Africa and Australasia to try and reconstruct the past history of *Phreatoicus* and the other freshwater Crustacea. I have come to the conclusion, however, that no useful purpose would be served by entering on such speculative inquiry, at least not in the present paper. For example, in the absence of fossil evidence, it is impossible to say whether Phreatoicids and Gammarids were present in former epochs in the more northerly parts of South Africa, and whether they arrived at their present habitats from the north or from "the lost land of Agulhas" and an Antarctic connection.

The question whether the ancient Gondwanaland was a zonal and more or less equatorial continent which was broken up by foundering of large portions, or a compact polar continent which has been sundered, is not one for zoologists to solve, but for geophysicists and geologists.

There is no denying, however, that in the case of an animal like *Phreatoicus*, dependent on the anastomosing of the river systems or widespread paludine conditions for its dispersal, the acceptance of the Wegener hypothesis would be welcome. (Barnard, **7**).

The fossil *Phreatoicus* is exceedingly important because it disposes of Smith's theory of a migration from the Northern Hemisphere via the Andes and Antarctica (**33,** p. 69, and "Naturalist in Tasmania," 1909) and shows that the tribe is both palaegenic and austrogenic. And *Phreatoicus* is the only instance we have of an animal with wide and discontinuous present-day distribution (Gondwanic) combined with clear palaeontological evidence.

V. Summary.

1. Further evidence of the affinity of *Phreatoicus* and *Asellus* is given in the modification of the 4th peraeopod in the ♂, the shape of the 1st oostegite, and the development of dorsal processes in the embryo.

2. A general account of the Biology of *Phreatoicus capensis*, including a curious habit of aestivation, and certain tendencies to variation is given.

3. *Phreatoicus capensis* is shown to be extraordinarily closely allied to *P. australis*. These two forms are regarded as being the direct descendants of the ancestral stirps represented by the fossil species *wianamattensis*.

4. A freshwater Isopod of the family *Jaeridae* is described, having affinities with the Australian genus *Heterias*.

5. Several new species of "blind" Gammarids are described; the eye of these "blind" species is histologically examined. The localised habitat of these "blind" species as contrasted with the wider distribution of the single black-eyed species is discussed.

6. It is noted that *Phreatoicus capensis* is confined to old and mature valleys in the less highly tilted mountains and is not found at the present day outside the limits of the effective deposition of moisture from the clouds formed by the south-east Trade winds.

7. It is pointed out that the finding of a fossil species of *Phreatoicus* not only shows that the tribe was austrogenic as well as palaegenic, but also puts out of court the theory of a migration of northern Crustacea via the Andes into Australasia.

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Note.—Since this paper went to press I have been able to consult the papers of Nicholls and Milner, Glauert, and Nicholls (J. and Proc. Roy. Soc. West. Austr., vol. x, pp. 23,

49, and 91, 1924), in which recently discovered representatives of the *Phreatoicidae* are described. These new finds, however, do not materially affect my main conclusions, at least not as regards South Africa, and I have therefore left my paper as originally written. As to the affinities of this family, my studies have tended to support Chilton's view of the very close relationship to the *Asellidae* in all essential characters, and I follow Chilton in maintaining that the resemblances to the Amphipoda, though interesting, have been exaggerated.

EXPLANATION OF PLATES.

PLATE V.

Bird's-eye view of relief model of the south-west portion of the Cape Province (in South African Museum), showing mountain ranges, northernmost limit of south-east clouds (dotted line), and localities of Freshwater Crustacea. (Vertical scale four times the horizontal.)

The letters correspond with those of the localities discussed in the section on Topography, p. 189, *sqq*.

PLATE VI.

FIG.

1. A mature valley on Table Mountain, the haunt of *Phreatoicus capensis*, *Gammarus capensis*, and *G. auricularius*.
2. A *Phreatoicus* pool in a similar valley in the Hottentots Holland Mountains.

PLATE VII.

1. Pits formed by *Phreatoicus* in the mud at the bottom of a dried-up pool in the Hottentots Holland Mountains.
2. Portion of a youthful stream on Table Mountain, the haunt of *Gammarus nigroculus*.

PLATE VIII.

1. Valley of the Steenbras River. Summit of Kogelberg obscured by cloud in right-hand distance. Locality for *Phreatoicus*, *Gammarus*, and *Protojanira*, indicated approximately by point of arrow.
2. A mature valley in the Hottentots Holland Mountains in which the pool figured in Plate VI, fig. 2, occurs.

PLATE IX.

Phreatoicus capensis.

1. Vertical longitudinal section of stomach, diagrammatic, with dotted lines indicating positions of sections 2–12.

FIG.

2–12. Vertical transverse sections of stomach, semi-diagrammatic, from the positions marked with corresponding numbers in fig. 1. The hepato-pancreatic glands in figs. 7 and 8, and their forward extensions in figs. 3–5 are omitted.

13. External view of embryo to show dorsal appendages.

LETTERING.

a_1 a_2	1st and 2nd antennae.
ap.	dorsal appendage.
d.l.	dorsal lamina.
h.	opening of hepato-pancreatic gland into stomach.
hep.	hepato-pancreatic gland.
l.c.t.	lateral cardiac tooth or triturating pad.
m.	bifurcate muscle from medio-ventral tooth.
m.d.t.	medio-dorsal cardiac tooth.
mx.	2nd maxilla.
mxp.	maxilliped.
m.v.t.	medio-ventral tooth.
oc.	eye.
sm.v.r.	submedian ventral ridges.
urop.	uropod.
v.c.t.	ventral cardiac tooth or striate ridge.
v.g.	ventral groove.
v.l.	ventral lamina.

PLATE X.

FIG.

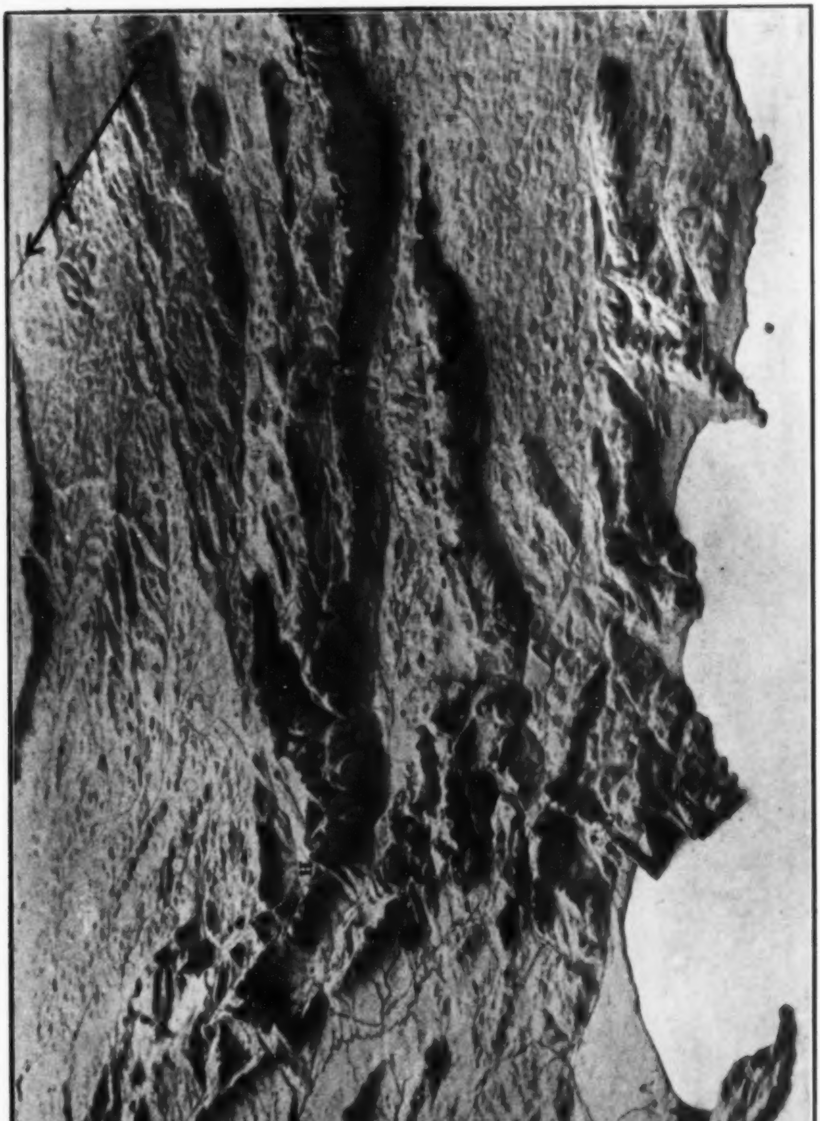
1.	*Gammarus*	*capensis* Brnrd.	4th right side-plate.		
2.	,,	*nigroculus* Brnrd.	,,	,,	
3.	,,	*auricularius* Brnrd.	,,	,,	
4.	,,	*crassicornis* Brnrd.	,,	,,	
5.	,,	*tulbaghensis*, n. sp.	,,	,,	
6.	,,	*aurantius*, n. sp.	,,	,,	
7.	,,	*seticornis*, n. sp.	,,	,,	
8.	,,	*spinicornis*, n. sp.	,,	,,	
9.	,,	*kogelensis*, n. sp.	,,	,,	
10	,,	*granulicornis*, n. sp.	,,	,,	♀
11.	,,	,,	,,	,,	♂
12.	,,	*nigroculus*, var. *persetosus*, n.v.,	2nd antenna ♂		
13.	,,	*auricularius* Brnrd.	3rd–5th joints 2nd antenna ♂.		
14.	,,	*crassicornis* Brnrd.	,,	,,	
15.	,,	*tulbaghensis*, n. sp.	,,	,,	
16.	,,	*aurantius*, n. sp.	,,	,,	
17.	,,	*seticornis*, n. sp.	,,	,,	
18.	,,	*spinicornis*, n. sp.	,,	,,	
19.	,,	,,	,,	,, (immature).	
20.	,,	*granulicornis*, n. sp.	,,	,,	
21.	,,	*kogelensis*, n. sp.	,,	,,	

PLATE XI.

1. Horizontal (longitudinal) section through one-half of head of *Gammarus capensis*.
2. Vertical (transverse) section through one-half of head of *Gammarus auricularius*.

Lettering.

c.	chitin.
c.o.c.	circumoesophageal commissure.
g.o.	optic ganglion.
hyp.	hypodermis.
m.	muscle.
m.l.	median line of head.
n.o.	optic nerve.
oc.	eye.
oes.	oesophagus.
sin.	blood sinus.
s.o.g.	supraoesophageal ganglion.



S.W. CAPE PROVINCE.

Neill & Co., Ltd.

Fig. 1.

Fig. 2.

Photos K. H. B.

Neill & Co., Ltd.

Fig. 1.

Fig. 2.

Photos K. H. B. Neill & Co., Ltd.

FIG. 1.

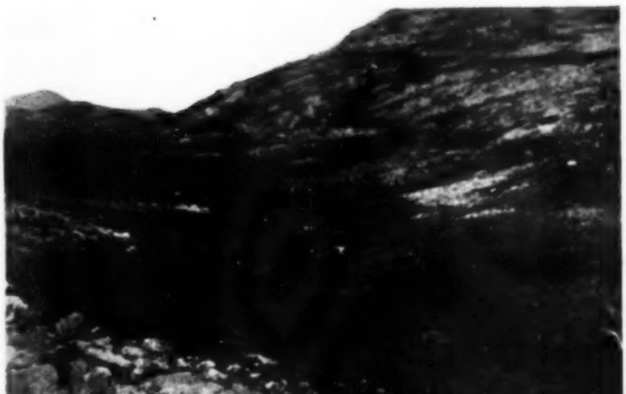
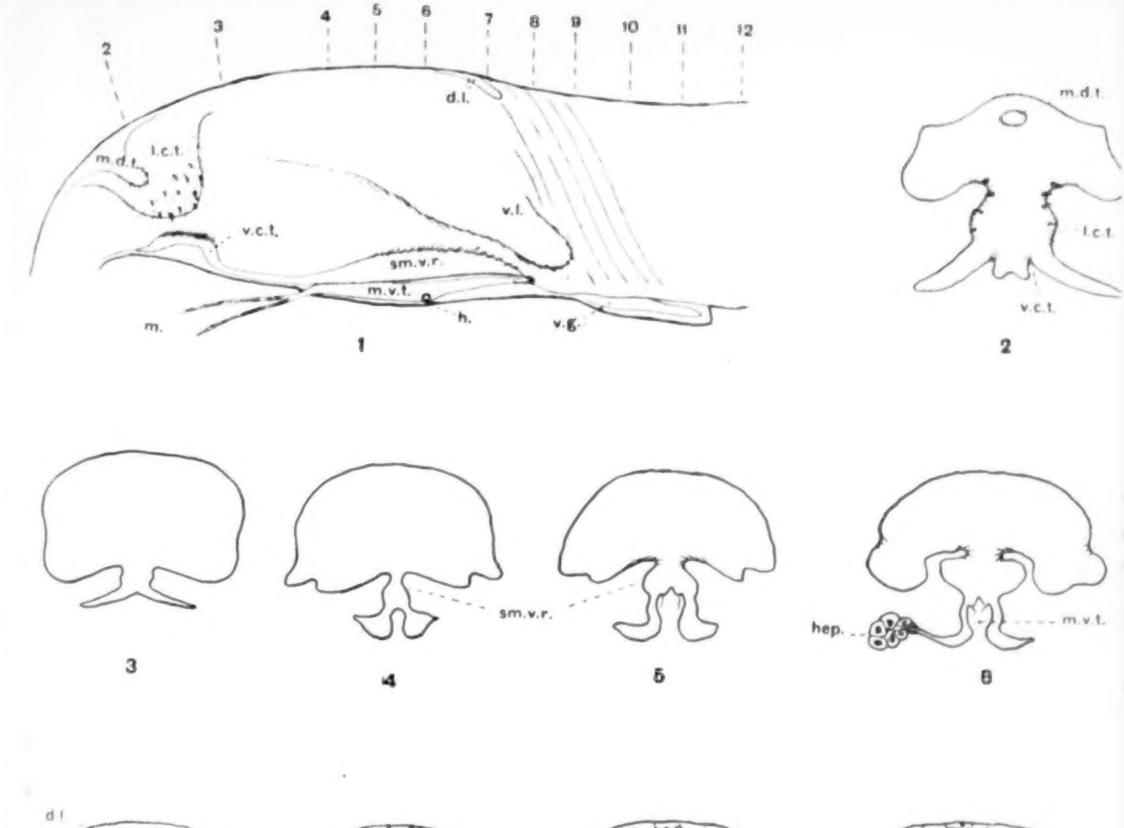


FIG. 2.

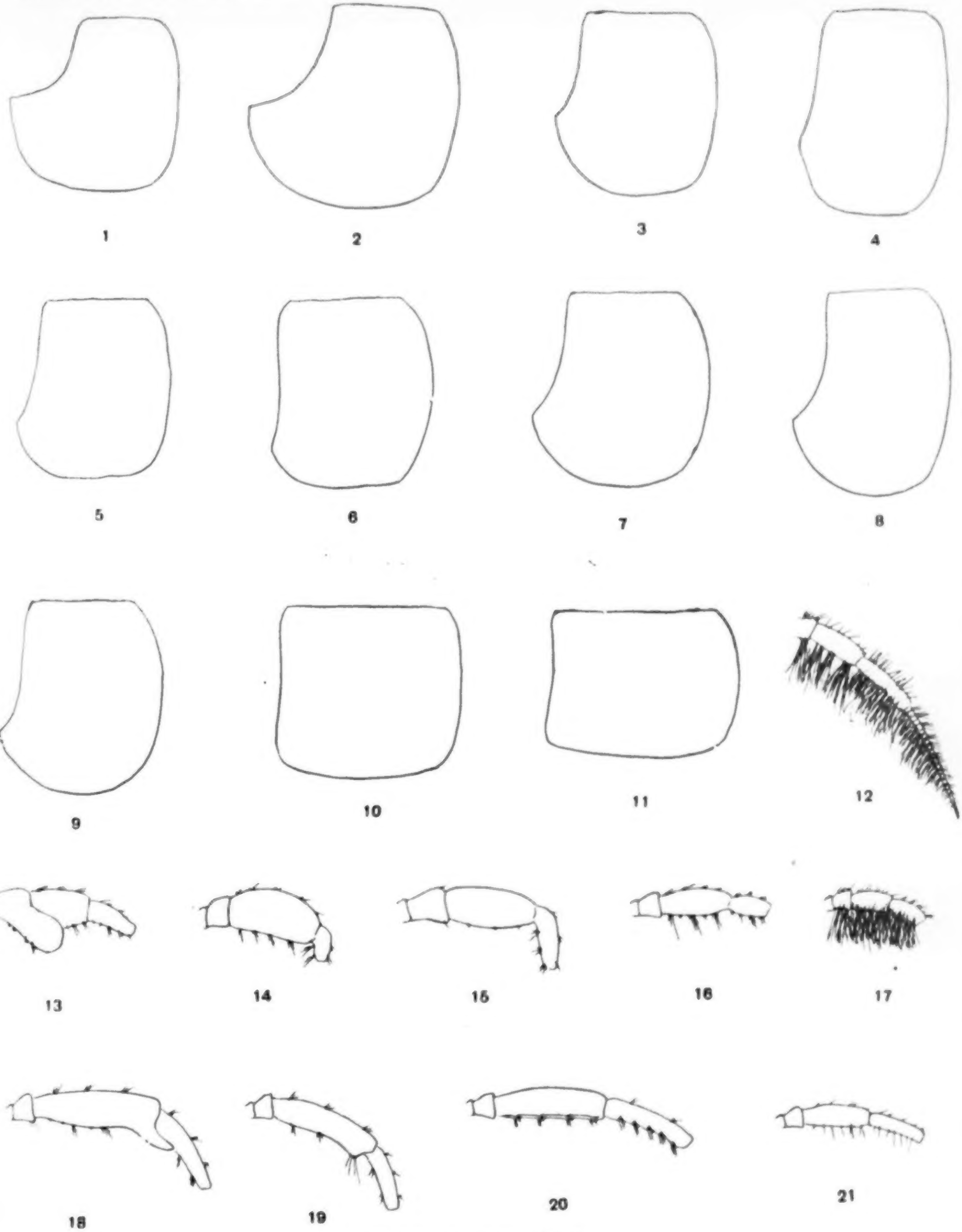
Photos K. H. B. Neill & Co., Ltd.

Tra

del. K.



PHREATOICUS CAPENSIS



SPECIES OF GAMMARUS.

del. K. H. B. *Neill & Co., Ltd.*

NOTE ON AN OCCURRENCE OF DIAMONDS NEAR PORT NOLLOTH.

By W. A. Humphrey, B.A., Ph.D.

Diamonds were recently discovered in the neighbourhood of Port Nolloth by Capt. J. Carstens, by whose courtesy an examination of the occurrence was made possible.

The stones occur in an alluvial deposit of gravel of a somewhat unusual character. The sand- and gravel-beds are from six to eight feet in thickness, and rest upon a country rock of quartz schist. The gravel varies in the size of its constituents in different bands, and consists of well-rounded pebbles of quartz—both clear, milky, and opaque—quartzite of various colours, and quartz sand. With these are associated, though much less abundantly, agates in rounded pebbles, onyx, jasper, opal, chalcedony, garnets, and pale-green serpentine. Olivene occurs sparingly in small prismatic crystals, almost black in reflected light, but in transmitted light showing their beautiful characteristic green colour. Grains of a black carbonaceous mineral, resembling coke, occur very plentifully in some horizons, sometimes cemented together in irregular filigree aggregations. The cement is siliceous and contains minute grains of quartz. This carbonaceous mineral is among the lightest material of the gravel. Ilmenite also occurs in grains and small pieces.

The diamonds are usually well crystallised, very brilliant, and pure white in colour. The largest stone observed was in the form of a perfect octahedron. Smaller crystals showed perfectly formed dodecahedron faces combined with hexoctahedron bevelling edges. Some of the crystals were flattened. Slight traces of wear were apparent at the corners of some crystals. A peculiar feature of this occurrence is, that the beds of loose gravel are separated from each other by bands of the same material cemented into a conglomerate by a calcareous cement, thus giving a horizontal alternation of hard and soft bands. The hard bands seldom exceed three-quarters of an inch in width.

This probably points to a seasonal deposition of gravel in a river-bed, followed by a season of aridity, when the flow of water became scanty, finally drying up and leaving its alkaline residue to cement the topmost gravel layer under the influence of sun and atmospheric conditions.

Towards the bottom of the deposit is a coarse boulder-gravel, and this, in some places, is also cemented into a conglomerate in the same way as the finer bands.

The greatest depth of gravel is found in the centre of the stream-bed, and the country rock of quartz phyllite has been laid bare at the bottom of the deposit, and also at a higher level on both sides of it, although the gravel overlaps the old stream-bed and covers the rocky banks as well. The lateral extension of the gravel had not been ascertained at the time of the writer's visit; it extended on all sides of the excavation where work was being carried on.

The whole occurrence lies in the bed of what, in a rainy country, would be a stream. It is a fairly regular depression, extending some five miles inland from the sea. Its lower end is choked with sand-dunes. Its upper course is well defined, and has a breadth of from thirty to forty yards. Five miles from the sea a low watershed is reached, consisting of sand-dunes, from which the ground slopes eastwards to the Kammas River, distant about one mile. The local topography depends upon the distribution of a great mass of surface sand, disposed in dunes and ridges, and it may well be that the Kammas River is connected with the sea by means of a number of outlets consisting of old channels now choked with this sand, of one of which this laagte is the surface indication. Its present mouth lies some few miles farther to the south. At several points along the coast, between Port Nolloth and the mouth of the Kammas River, springs of fresh water occur on the beach, and in some cases below high-water mark, and these may possibly be, and indeed probably are, connected with the drainage system of the Kammas River.

It seems natural, therefore, to look to the Kammas River as the agency which deposited these gravel-beds, and to the basin of this river for the source of these alluvial diamonds. The diamonds, however, show slight traces of wear at the corners, which could only be brought about by long-continued abrasion and transport erosion; and this, the comparatively short Kammas River, which is only some fifty miles in length, would hardly have accomplished. The freshness of the olivene crystals somewhat discounts their presence in the gravel as being an indication of their original association with the diamonds, and garnets are found in the Port Nolloth and Steinkopf area abundantly in mica schists, and eclogites quite unconnected with diamondiferous rocks. In the absence of diamonds the presence of these minerals can be explained by reference to various local rocks having no connection with diamonds, but when found with diamonds in a gravel-bed they attain a greater significance. The theory that diamonds along the coastal belt may have been thrown up by the sea does not seem to the writer to be a possible explanation of this occurrence.

THE CHANGED CONDITIONS OF NAMAQUALAND.

By W. A. Humphrey, B.A., Ph.D.

(With Map.)

The river valleys and general topography of Little Bushmanland immediately to the south of the Orange River furnish considerable evidence relating to the past history of the country, notably

(*a*) that this portion of the country represents an extremely ancient land surface;

(*b*) that the present climatic conditions have probably persisted from very remote times;

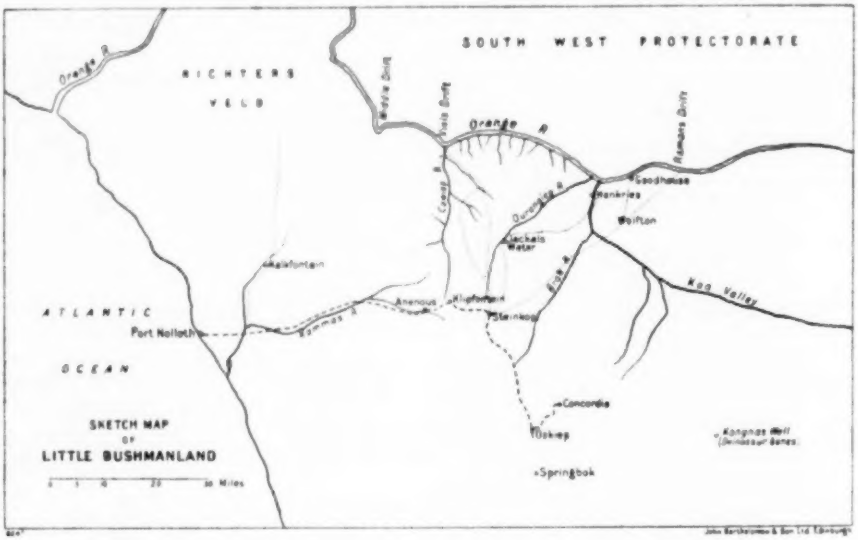
(*c*) that in earlier times still the rainfall over this area must have been very considerable.

From Viols Drift to Ramans Drift on the Orange River is a distance of some 60 miles. The tributaries of the Orange River on its southern bank between these two drifts, and the basin of the Kammas River, which reaches the Atlantic Ocean some 10 miles southward of Port Nolloth, supply the material for the conclusions of this paper.

Most of the tributaries of the Orange between Viols Drift and Henkries have courses of from 8 to 10 miles in length, and they are now confined to the belt of extremely rugged and mountainous country lying immediately to the south of the river, where they experience a fall of nearly 1000 ft., having cut out for themselves a series of narrow, tortuous, and deeply dissected valleys separated from each other by mountainous and broken country of extreme difficulty.

The streams cut across the geological formations, which consist of basic igneous rocks alternating with much-altered schists of varying character. The bottoms of these valleys are composed of bare country rock obscured at intervals by boulders from the adjacent mountains, the steep gradients having been unsuitable for the formation of alluvium or gravel beds. As the gradient becomes less steep some 5 or 6 miles from the Orange River, the valleys become filled from side to side with rivers of sand. This sand consists principally of grains of quartz, and as the country rock here consists of gabbroidal and dioritic rocks, which are free from quartz, this sand

must have come from country considerably further to the south, where the diorite gives place to granite. The valleys, traced upwards, become more and more choked with sand until they can be traced no further, and a topography conditioned by accumulated surface deposits takes the place of the old river valleys, with a general drainage towards the three longer tributaries of the Orange, namely, the Brak River and the Ourangiep and the Cowiep Rivers, which are still functioning, if intermittent streams, having their



sources in the high ground around Concordia, Steinkopf, and Klipfontein, where the rainfall is still sufficient to enable them to keep their courses open against the encroaching arid conditions of the intermediate area between Steinkopf and the Orange River.

It seems probable, therefore, that the shorter tributaries of the Orange, which now exist only as dry stream valleys in the steeply graded mountainous country adjoining the Orange River, originally had a considerable southward extension at some time when the rainfall was sufficient to enable them to cut out their beds as swiftly flowing streams of considerable volume, but that changed climatic conditions have resulted in the filling up and obliteration of their upper reaches; a new surface topography having been formed, related to the three major tributaries which have still been able to hold their own against the changing conditions.

These conditions are seen in active operation along the middle reaches of the Brak River in the eastern portion of the area under consideration. At Wolfton, 5 miles south-east of Henkries, the southern slopes of the mountainous belt forming the immediate valley of the Orange River are in process of being covered up by blown sand from the Twenty Mile Plain bordering them on the south. The southerly winds have blown up the sand into the mountain valleys, and in some cases sand passes have been made over the lower portions of the range. Over one such pass the road from Steinkopf to Goodhouse crosses the range, which further to the east loses its character altogether and becomes a series of disconnected mountain tops appearing from beneath the accumulated surface deposits of wind-blown sand.

The Twenty Mile Plain contains the middle reaches of the Brak River. It has been described by Rogers, who considers, on the evidence of deinosaur bones found in a well, and described by Haughton, that it represents an ancient river valley which has been gradually filling up with surface accumulations of sand from exceedingly remote times.*

It is a wide, gently sloping, sandy plain, bounded on two sides by rugged mountains which rise out of the sand as if it were a lake of water. On the southern side the sand extends up the lateral valleys of the Henkries Mountains much as water would, except that there is usually a slight slope up the valleys, and the indentations form sand gulfs and bays in the black masses of the mountains. Viewed by moonlight from the mountain slopes, and also in the glare of midday from a side valley, one might imagine one was looking over a peaceful estuary. The plain gradually narrows towards Henkries Water, 4 miles from the Orange River, and the fall becomes more pronounced. The northern mountain barrier, which is exposed to the prevailing wind in the dry weather, has been described above, with its long slopes of blown sand gradually covering the mountains with the rise of the valley floor as it is followed to the east.

Another example of the gradual filling up of a river valley owing to changing conditions of climate is afforded by the Kammas River, whose main branch roughly coincides in direction with the railway line from Steinkopf to Port Nolloth. In the search for permanent water, boreholes were put down by the Cape Copper Company at various points along the river bed, and although the water-level does not always indicate the bottom of the accumulations of sand and gravel, it affords a means of judging the relative depth of the old bed at various points. From Anenous to Fifteen Miles, on a descending gradient, the water-level increased in depth. At the latter place water was found at a depth of 143 ft. below the present

* Trans. Roy. Soc. S.A., 1915, "The Occurrence of Deinosaurs in Bushmanland," by A. W. Rogers; "On Some Deinosaur Remains from Bushmanland," by S. H. Haughton. S.A. Journal of Science, December 1922, "Post-Cretaceous Climates of Africa," Rogers.

surface, and the core still showed sand and river gravel, with thin bands of clay. This borehole is in a poort made by the river through the Augrabies Mountains, which still rise to the north and south of the poort to heights considerably over 1000 feet.

It seems probable that the chief agency in the filling up of the Kammas River Valley has been the river itself, and the process is still in active operation along its middle reaches. At Twenty-nine Miles is a well of something over 100 ft. in depth. At the time when the well had just been completed, a flood occurred, the effects of which were described to the writer by Mr Pearce, who was in charge of the work. At this point there is a convergence of flat watercourses, although this is by no means apparent to a casual eye, and on the day in question heavy thunderstorms were noticed raging in the mountains to the east and south-east round about Klipfontein and Kosies Berg. In the course of the afternoon three successive floods came down the sand laagtes from the north-east, east, and south-east, but spread out at Twenty-nine Miles into a lake-like expanse owing to the absence of any defined channel further down. Great quantities of sand and gravel were deposited over the whole flat. Such floods are still not uncommon at Twenty-nine Miles, which seems to be the extreme limit to which the Klipfontein branch of the Kammas River now functions as a running stream. At this point flood water sinks away in the sandy flats. It seems likely that the various sand plains lower down the river have been formed in the manner above indicated, during a period when the annual rainfall was decreasing, and the volume of water became too small to force its way to the sea.

The Kalkfontein branch of the Kammas River, which flows in from the north at Eight Miles, although now dry, has at one time cut a series of fine gorges through the quartzites of the Augrabies Mountains. In July 1925 it came down in spate, washing away a portion of the railway at Eight Miles, this being the first time that water had been seen in this channel within living memory. An examination of the lower reaches revealed the fact that the stream had formed several new channels through the sand-dunes and valleys near the coast, although the bulk of the water had kept to the old bed. This fact is interesting in view of the discussion on alternative courses for the lower Kammas River mentioned in a previous paper.*

Deposits of marine shells were found among the sand-dunes several miles from the present coast-line, which in some cases seemed a natural distribution along an old beach. It seems probable that we have here to do with a gradually rising coast.

The Brak River, during the heavy rains of July 1925, carried water to the Orange River for the first time within the memory of the Hottentots

* "Note on the Occurrence of Diamonds near Port Nolloth," *ibid.*

living at Henkries. The writer was fortunate enough to be at the junction of this river with the Orange at the moment when the flood came down. Although there was nothing like a head or wall of water, yet its approach was heralded by a loud, roaring sound, and within two minutes of the first appearance of the water the stream bed was a roaring torrent of a rich red colour. The alluvial mud banks brought down by the floods of the Orange in March 1924 blocked its egress, but in ten minutes it had torn its way through this barrier, and after two hours had formed a wide delta in the shallow waters of the Orange River, forcing the stream on to the north bank. Along the bed of the Brak River, which the writer traversed for some 30 miles from its mouth, there is nothing like the flat alluvial spread of the Kammas River, but a fairly well-defined course all the way with a sandy bed above Wolfton to the mountains bounding the Twenty Mile Plain on the south. It is evident that this river, intermittent though its flow is, and although it is sometimes perfectly dry in its lower course for years together, is yet able to hold its own against the wind-borne sand; but it must be remembered that although the Twenty Mile Plain may be classed as an area possessing an arid climate, yet its conditions are by no means desert, and in favourable seasons it supports a luxuriant growth of grass, which even when dry holds the sand in check, except in successive seasons of drought, while there is a considerable perennial vegetation of drought-resisting succulents.

The river has evidently just been able to keep pace with the gradual infilling of the old valley, keeping open a shallow bed on the surface, but unable to prevent the gradual filling in of the valley floor. Doubtless, like the Kammas River, the Brak is also depositing much detritus along its middle course, and great accumulations of sand and gravel exist along its banks above the Twenty Mile Plain.

It is significant that this river, with a flow in its lower reaches of perhaps two days in forty years, is able to keep open its course against the accumulating wind-borne sand, and illustrates the extreme slowness of some of the processes of Nature in its work of remodelling and recasting the physical features of the land; and one can form some conception of the time it has taken to cover up to a depth of 112 feet the bones of the deinosaurs which were referred to as having been found in this neighbourhood.

The question of the age of this old land surface is not easy to decide in the absence of more detailed traversing than has yet been done.

The presence of Dwyka conglomerate near Viols Drift, which elsewhere underlies the Ecca Shales and Beaufort Beds of the Karroo system, might lead one to suppose that we may have here before us an area where the Karroo system was once deposited, and which has since been almost entirely removed by denudation. This occurrence forms part of a large development

of Karroo rocks occupying the area immediately to the north of the Orange River,* and no other rocks belonging to this geological system have as yet been observed in Namaqualand.

The presence of deinosaur bones almost on the old pre-Karroo land surface at Kangnas would, however, indicate that, while the Beaufort beds were being laid down some 200 miles to the south-east, this area was a land surface, and probably separated the great Karroo basin from the area of contemporaneous deposition to the north-west across the present basin of the Orange River.

Should detailed mapping fail to show any traces of post-Karroo rocks in this area, one would be justified in concluding that probably it represents a land surface which has been exposed to denudation since the deposition of the lower Karroo beds, and possibly even longer.

The presence of Beaufort fossils so near the surface among superficial accumulations would point to the supposition that the climate during that immense period has not sensibly differed from that obtaining at the present time. It also opens up fascinating lines of conjecture into the migratory habits of the deinosaurs, and into the tectonic disturbances which finally emptied the Karroo lake, in which the fact that the Koa Valley and Brak River still constitute the principal line of drainage from the Kenhardt district westward would be a not unimportant factor.

* See Geol. Maps, Range and Wagner.

NOTES ON THE RIVER-SYSTEM OF SOUTH-WEST GORDONIA.

By S. H. Haughton, B.A., D.Sc.

(With Plates XII–XIV and two Charts.)

(Published by permission of the Hon. the Minister for Mines.)

A glance at the topographical map of Gordonia will show that the Molopo River, in the last sixty miles of its long journey to join the Orange, pursues a somewhat irregular course. In the course of this last sixty miles it falls a vertical height of about 1150 feet, more than half of this drop occurring in the last eight miles. It passes through sandy and through rocky country in a sparsely-inhabited region. It contributes little, if any, water to the mighty volume which the Orange River carries, but it is of a different calibre from, and offers more scope for study than, the majority of the other tributaries of the Orange west of the Vaal. During the course of geològical survey work in Gordonia in 1925 I was enabled to make a number of observations on the nature of its valley, and these are offered here as a contribution to the study of past conditions in that area.

From Zwartmodder down to Cnydas, a distance of nearly thirty miles, the Molopo takes a southerly direction in a somewhat narrow, flat-bottomed valley which is flanked by steep banks of granite, gneisses, and older rocks of the Kheis System overlain by horizontal sandstones and quartzites of the Zwartmodder Beds. From Zwartmodder to a point about a mile north of Smalvisch this escarpment of Zwartmodder Beds closely follows the sides of the valley; but on the right bank at the latter point the escarpment suddenly bends to the west for a couple of miles and then turns southwards to end at a point some three miles north of Molopo Kop. Thus between Smalvisch and Toeslaan there is a broad belt of older rocks exposed to the west of the Molopo. At the time of my visit a low wall thrown across the river at Smalvisch had dammed back an extensive sheet of water. Below this wall the valley silt was being irrigated to beyond the Toeslaan boundary, whilst at Toeslaan and onwards to Cnydas there were several extensive pools in the river. No water was, however, flowing.

At Cnydas the valley trends westwards for three miles and then turns southwards again to Jansies Puts. Most of this stretch is picturesque, large trees flourishing in the valley bed and steep walls of shattered rock

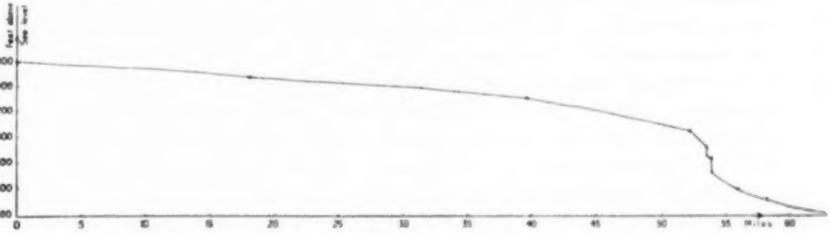
flanking it on either side down to a point west of Biesjespoort. From Jansies Puts the valley is a somewhat ill-defined sandy depression westwards to Riemvastmaak, from whence nearly to the Orange River it becomes a picturesque and winding kloof with all the characters of a rejuvenated

Sketch plan of river-system of S.W. Gordonia. The dotted line shows the edge of the escarpment of Zwartmodder Beds.

stream. The valley floor in its final two miles is choked with sand and largely covered with scrub, and its sides are flanked by barren and inhospitable rounded knobs of granite and gneiss.

From Zwartmodder to Smalvisch the valley falls 120 feet in 18 miles; from Smalvisch to Jansies Puts 180 feet in 21½ miles; from Jansies Puts to Riemvastmaak 250 feet in 12½ miles; and from Riemvastmaak to the Orange River 600 feet in 7½ miles. A pace-traverse with an aneroid was

made of the last-named stretch; and from it the profile given herewith has been constructed. It will at once be seen that, as to grade, the river between Zwartmodder and the Orange can be divided into two portions: (1) a portion above Riemvastmaak, characteristically a low-grade, scarcely-defined, sandy channel following a better-defined low-grade depression with a fair number of pools of water, and (2) a valley of variable grade below Riemvastmaak, with two distinct falls, a stretch of rapids, and a section which runs in a narrow gorge with high perpendicular sides—the last section abruptly changing to the final short portion, which is a low-grade sandy stretch bordered by low hills. In the high-grade portion, and especially near the gorge-section, the lateral tributaries have hanging valleys where they meet the Molopo. Elsewhere (*i.e.* above the falls and below the lower end of the gorge), the lateral valleys are of even grade with the main stream.



Exaggerated profile of Molopo River between Zwartmodder and Orange River.

That the Molopo was at some previous date an even-graded stream in its lower reaches is evidenced by the very interesting patches of river-gravels and pieces of river-cut terraces which still remain along its course. These will be considered in some detail.

On the left side of the valley just below Smalvisch House, between the river and the plateau of Zwartmodder Beds to the east of it, there are remnants of a peneplaned surface cut in the sillimanite rocks, sloping towards the river at an angle of between one and two degrees. The terrace stands at its highest about 80 feet above the Molopo, and is capped by a few feet of calcareous tufa containing pebbles and boulders—the larger ones, of quartzite, showing well-defined chattermarks. To the west of the river, and about ¾ of a mile from it, there are further remnants of this peneplain covered with fragments of Zwartmodder quartzite, the nearest outcrop of which lies nearly two miles away. On the surface of this terrace, mixed with the loose gravel, were found some rough "bouchers" and one extremely fine example of a laurel-leaf boucher made of red quartzite, 9 inches long, 4 inches broad, and about 1½ inches thick, its edge almost straight as a result of fine secondary chipping.

North of the bend in the river east of Riemvastmaak there is a gravel-covered terrace at about 50 feet above the level of the present bed. The loose pebbles forming the gravel are not graded but are well rounded except where broken by percussion. They are mainly of quartzite, but contain small pieces—up to an inch in diameter—of banded jasper.

Below Riemvastmaak, on the right bank of the river between the first and second falls, and at a height of about 1970 feet above sea-level, there are a number of rounded pebbles (mostly of quartzite, but a few of jasper) lying on a flattened surface, which can only be interpreted as the remnant of an old terrace.

Half a mile below the present position of the second fall, at a height of 1950 feet, there is a small hillock to the right of the river capped by a large number of loose pebbles. These range in size from 10 inches in diameter to that of a pigeon's egg, the larger ones being all of Zwartmodder quartzite, the smaller partly of vein quartz and red jasper. The pebbles are smooth and many have flattened faces.

In the gorge section of the valley, and just below it, the peneplanation of the strip on both sides of the river at the top of the steep walls of the gorge is very obvious; and this planed surface lies at almost the same height as the last-named patch of gravels. Below this stretch the country immediately bordering the river is below the level at which one would expect to find traces of a continuation of this terrace; and no lower terraces are seen. One can therefore conclude that, at the time of formation of the terraces, the river was of even grade from Zwartmodder to the Orange.

That the falls of Riemvastmaak are related to the Aughrabies Falls of the Orange seems undoubted. The long narrow gorge through which the Orange flows below the Aughrabies Falls is indicative of a prolonged period of backward erosion of the falls. At some point in time an even-graded Molopo joined an even-graded Orange just above a large fall in the latter. The retrogression of this fall upstream—had there been no flow of water in the Molopo—would have left the Molopo as a hanging tributary. The fact that it has been able to cut its fall back 7½ miles whilst the Orange has cut its fall back 14 miles shows that, for a length of time after the falls of the Orange had reached the Molopo mouth, this "dry river" carried a body of water capable of exerting considerable erosive power. In this connection it is interesting to note that in the section of the Molopo below the gorge the bank of the river consisted of a deposit up to 15 feet in height of bedded sandy gravel and gravelly silt, material deposited in the lower reaches by the waters as the slope of the bed suddenly decreased.

It is inconceivable that active cutting-back of the Molopo Falls is taking place to-day; and two questions immediately arise: (1) At what period did erosion cease? (2) What caused the cessation of the active flow of the

river? Answers to these questions are difficult to give, but certain facts help towards their solution.

The tributary valleys of the Molopo below Zwartmodder are short, rising on the scarps of the Zwartmodder Plateau and flowing with even grade to the Molopo above the falls, but forming hanging valleys in the section between the upper fall and the lower end of the gorge. They were thus tributaries which carried water before the rejuvenation of the main stream, but were unable, after that event, to keep pace with the downward erosion of the Molopo. On the other hand, the Kourop River, which rises on the plateau and enters the Orange west of the Molopo, has no falls in its course but runs in a steeply-graded bed; and the Bak River, near the S.W. African border, falls rapidly from Aries, and still more rapidly in a series of cascades from west of Kourop Trigonometrical Beacon, to the Orange. Both, like the lower reaches of the Molopo, have granite as their rock-bed; and the difference between the grade of the Kourop and that of the tributaries of the Molopo below Riemvastmaak is a very striking one. The conclusion is drawn that, during the time that the Aughrabies Falls took to recede from the Bak River to some point between the Molopo mouth and their present position, the Kourop and Bak Rivers (which now carry very little running water) were able to keep pace with the downward erosion of the Orange; and that the tributaries of the Molopo at Riemvastmaak, maintaining their former grade for a longer time, have been unable to reduce their levels to the same extent. In other words, the downward erosion in this area has taken place progressively, stream by stream, from west to east as a result of the cutting back of the Aughrabies Falls; and the Molopo bears the same relation to its tributaries as does the Orange to the Bak, Kourop, and Molopo.

Certain interesting points arise from a study of the Orange River below the area with which we are immediately concerned. According to Lewis (Rept. Director of Irrigation, 1912–1913), from the Aughrabies Falls down to Zendlings Drift, a total distance of over 350 miles, the river runs in a deep narrow gorge, with generally steep slopes on both sides rising to as much as 2000 feet from near the water's edge. There is very little irrigable land in this stretch of the valley; and in the neighbourhood of Houms Drift the river has a considerable fall over a rocky bed. From Zendlings Drift to the sea, the valley becomes wider and more sandy, and the irrigable patches increase in number and extent. Further, the tributaries of the Orange on the south side run—in the last two or three miles of their courses—in deep narrow rocky gorges, descending rapidly from the wide sandy plains in which they run over the "bult" which lies along the south side of the main stream. Rogers (Trans. Roy. Soc. S. Afr., v, 1915, p. 265) describes the Kangnas Valley, which is part of the system which enters

the Orange at Henkries. The last $3\frac{1}{2}$ miles of this valley drops about 400 feet to the Orange, whilst above Henkries Water the valley is wide, open, but sloping at the surface. This portion of the valley, however, is filled with locally-derived sandy debris to a depth of at least 112 feet, and may well be an extremely old, possibly Mesozoic, valley which has been filled by sand. The floor of the valley below Henkries Water, too, is covered by coarse sand, grit, and calcareous tufa, the rock bottom only appearing near the Orange River. Thus the true profile of the valley bottom is obscured; but it can be stated that, in a general way, it probably conforms to the profile shown by the lower reaches of the Bak River.

It is important to notice that it is only in the final few miles that the Henkries Valley shows this steep gradient. In the main portion of the long valley, active downward erosion had ceased by Upper Cretaceous * times and, since that time, "the stream was no longer able to keep the channel open; the valley became filled in with quartz and felspar grit, and ever since then the process of accumulation has, on the whole, continued; the climate has not become sufficiently humid to supply a stream which could re-excavate the valley" (Rogers, S. Afr. Journ. Sci., xix, 1922, p. 8). The lower, and steep, part of the valley is gradually being obscured by wind-blown sand; but, subsequent to Upper Cretaceous times, there must have been a period of active downward erosion in this portion of the valley, a period which has now ceased.

According to Dr. Humphrey, the northward-flowing tributary valleys of the Orange River east of Henkries show similar features to those of the Henkries Valley.

These short, steep, lower portions of the valleys are obviously correlated with the active downward erosion of the main stream; and the question suggests itself: Is the rejuvenation of these short portions of valleys which, for most of their length, approximate to an even grade in any way connected with the recession of the Orange River Falls past their mouths? There are no river gravels thereabouts to indicate that the Orange ever flowed at the general height of the surrounding plain; but they are scarcely to be expected, for, had the main stream ever flowed at that level, it would have been at so remote a period that the gravels would have disappeared. But the presumption, from the evidence afforded by the old plain and by the present gorge of the Orange, is that the main stream has cut down to its present level in that region since Upper Cretaceous times, and that we are dealing here with a rejuvenated stream. The canyon-like nature of its valley is due to the fact that nearly all the water carried in it is allochthonous, the arid nature of the climate forbidding lateral erosion. This

* The age of the valley floor is fixed by the discovery of Upper Cretaceous Dinosaurs at the base of the sands at Kangnas. Rogers, Trans. Roy. Soc. S. Africa, v, 1915, p. 265.

post-Upper Cretaceous rejuvenation in the Henkries area must have been due, either to a general uplift of the land or to the recession of a pre-existing fall from farther down stream. The evidence is insufficient to enable it to be decided which of these two causes was the operative one.

Rogers (*loc. cit.*, 1922) dates the diminution of rainfall in the Henkries Valley in " late Cretaceous or early Tertiary times." It is obvious, however, from the nature of the Molopo gravels, that the active erosion in S.W. Gordonia and the cutting-back of the Molopo Falls extended into much more recent times. In the case of the Kourop it is important to note that the active eroding agent was water derived entirely from a small area near the Orange, although much of the Molopo water may have come from more remote regions in its catchment area. It seems clear, however, that humid conditions continued in Gordonia to a far later date than they did further west; but that, even here, conditions were not constant is evidenced by the last three miles of the Molopo Valley. Here, as has been pointed out, are patches of bedded sand and gravel in the valley which are partly cut into by the stream-bed, indicating that alternations of deposition and erosion must have taken place in the area.

It is unfortunate that no evidence has as yet been obtained as to the age of the gravel terraces of the Molopo and of the Orange near Upington. The former certainly antedate the recession of the Molopo Falls to their present position; and they indicate an uplift of the area of about 50 ft. It seems certain, however, that they cannot be connected with the " noticeable river terraces " described by Lewis (*loc. cit.*) as occurring along the lower reaches of the Orange south of Aussenkehr and in the stretch between Zendlings Drift and Arries Drift, nor with the " raised beaches " which occur at intervals south of the Orange along the west coast. Dr. Rogers informs me that the former go up much more than 100 feet where the Orange debouches from the Richtersveld; and they must be connected with uplift at the coast (which, from certain fossil evidence, seems to be post-Miocene). Unless, however, the uplift was such that the whole land from Upington westwards was tilted towards the sea, the rate of downward erosion would not be uniformly increased all over the area, and the gravels of the Molopo would not be due to the same uplift as gave rise to those of the Lower Orange.

Second fall of Molopo below Riemvaatmaak, seen from right bank of river.

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A view of north end of gorge section of the Molopo River.

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Looking northwards up valley of Bak River, from near Bokseputs, showing valley cut through plateau of Zwartmodder Beds.

View of entrenched portion of Molopo River, seen from near Riemvastmaak.

North end of gorge section of Molopo River, south of Riemvastmaak. View looking south.

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COLOUR AND CHEMICAL CONSTITUTION.

Part XXI.—A Study of Methyl Derivatives of the Phenolphthaleins.

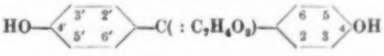
By James Moir.

A.

Part XI of this work (1921, ix, 129) was devoted to a similar study of bromine derivatives of *p–p′*-phenolphthalein, and formed at that time the most extensive study of the phenomenon of " loading " in a single coloured substance ever performed up to that date.

Inasmuch as even then the series could not be completed because a number of brominated phenols refused to give phthaleins, I have persevered towards a solution, and, finding that the group methyl has less disturbing action than the bromine atom on phthalein formation, have succeeded in making almost the whole of the possible methyl derivatives of phenolphthalein, and thereby found out that the effect of " loading " is perfectly regular and additive. The following table gives the observations. The numeration of the substances follows the diagram given.

Table I.



p–p′- or ordinary phenolphthalein (λ 554).

Ordinary Name of Substance.	Nature of " Load."	λ in Aqueous Alkali
1. Phenolorthocresolphthalein	3-methyl	562
2. Phenolmetacresolphthalein	2-methyl	569
3. Orthocresolphthalein	3–3′-dimethyl	570
4. Metacresolphthalein	2–2′-dimethyl	583
5. Phenol-*vic.*-orthoxylenolphthalein	2–3-dimethyl	575
6. Phenol-paraxylenolphthalein	2–5-dimethyl	574
7. Phenol-*vic.*-metaxylenolphthalein	3–5-dimethyl	570
8. *Vic.*-metaxylenolphthalein	3–3′–5–5′-tetramethyl	581
9. Paraxylenolphthalein	2–2′–5–5′-tetramethyl	590

TABLE I.—*continued.*

	Ordinary Name of Substance.	Nature of "Load."	λ in Aqueous Alkali.
10.	*Vic*-orthoxylenolphthalein	2-2′-3-3′-tetramethyl	593
11.	Phenoltetrahydroalphanaphthol-phthalein	2-3-*cyclo*-butyl	584
12.	Phenolthymolphthalein	2-methyl-5-isopropyl	578
13.	Phenolcarvacrolphthalein	5-methyl-2-isopropyl	580
14.	Thymolphthalein	2-2′-dimethyl-5-5′-diisopropyl	597
15.	Carvacrolphthalein	5-5′-dimethyl-2-2′-diisopropyl	601
16.	*p-p′*-Phenolalphanaphtholphthalein	2-3-benzo	601
17.	*p-p′*-Alphanaphtholphthalein	2-3-2′-3′-di-benzo	650
18.	Phenol-8-hydroxyquinolinephthalein	2-3-pyridino	598
19.	Phenol-6-iodoorthocresolphthalein	3-methyl-2-iodo	576

Table II contains the calculated additive values of each load, including the data from Part XI.

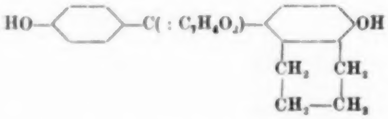
TABLE II.

3- and 5-methyl	7½	2- and 6-methyl	13½
3′- and 5′-methyl	6½	2′- and 6′-methyl	12½
3- and 5-chloro	7	2- and 6-chloro	13
3- and 5-bromo	8	2- and 6-bromo	15
3- and 5-iodo	9	2- and 6-iodo	16
3′- and 5′-chloro	6	2′- and 6′-chloro	12
3′- and 5′-bromo	7	2′- and 6′-bromo	14
3′- and 5′-iodo	8	2′- and 6′-iodo	15
3- and 5-isopropyl	10	2- and 6-isopropyl	18
3′- and 5′-isopropyl	8	2′- and 6′-isopropyl	15

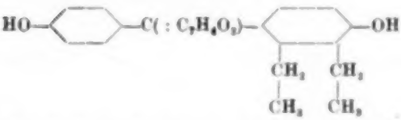
From Table II the absorption of any complex halogen- or methyl- or isopropyl-derivative of phenolphthalein can be calculated by adding to the number 554 in succession the corresponding figure for each load.

The whole of the data in Table I agree with this scheme within the experimental error. The solution of the problem is a complete one, since Table II covers all possible cases.

The most interesting result concerns the effect of closing a ring in phenoltetrahydroalphanaphtholphthalein (λ 584).



The corresponding unclosed structure is 2–3-diethylphenolphthalein.



Now the 2–3-dimethyl combination has an effect of +20 or +21 and the 2–3-diisopropyl combination one of +27 or +28, so that we can safely infer the 2–3-diethyl combination to have an effect of about +23. The calculated λ is 577. The effect, therefore, of uniting two adjacent ethyl groups into a *cyclo*-butyl ring is only +7. This small effect is in agreement with earlier data on saturated loads, *e.g.* the slight difference between the absorptions of dihydroxyxanthhydrol and succinylfluorescein.

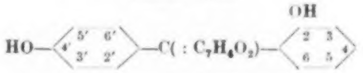
On the other hand, when an unsaturated ring becomes attached, the change is considerable (λ 575 for No. 5 of Table II and λ 601 for No. 16, the difference in constitution being the replacement of two pairs of hydrogens by the ring-section =CH—CH=). When it occurs in both rings, the effect is doubled (λ 593 for No. 10 and λ 650 for No. 17).

B.

Similar Derivatives of Orthopara-phenolphthalein.

Phenols which are substituted in the para position cannot, of course, give ordinary phthaleins: with phthalic acid they give fluoranes. When combined with phenolphthalic acid (see Parts II and III, 1918) they give derivatives of *o*–*p*′-phenolphthalein. The following Table gives the result of observation of such substances.

Table III.



Orthoparaphenolphthalein (λ 552).*

	Ordinary Name of Substance.	Nature of "Load."	λ in Aqueous Alkali.
1.	Phenolparacresolphthalein	5-methyl	563
2.	Phenol-*asym.*-metaxylenolphthalein	3–5-dimethyl	573
3.	Phenol-*asym.*-orthoxylenolphthalein	4–5-dimethyl	578 †
4.	Phenolparabromophenolphthalein	5-bromo	559
5.	Phenolbromoorthocresolphthalein	3-methyl-5-bromo	570
6.	Phenolbromoparacresolphthalein	5-methyl-3-bromo	569
7.	Phenol-*symm.*-metaxylenolphthalein	4–6 dimethyl	572
8.	Phenolpseudocumenolphthalein	3–5–6-trimethyl	581
9.	Phenolbetanaphtholphthalein	5–6-benzo	570 broad
10.	Phenol-2-alphanaphtholphthalein	3–4-benzo	612

* See Part XX, 1926. † The 5–6 isomer does not form, owing to "protection."

The additive values appear from this to be :

3- and 5-methyl=11 ; 3- and 5-bromo=7 ; 4-methyl=13 ; and 6-methyl=7.

An interesting experimental point is that 1-3-5-xylenol would not form a phthalein, although it has a free para position. The sole product was tetramethylfluorane ($\lambda\lambda$ 480 and 505 in conc. H_2SO_4). No. 7 above is therefore also assumed to be as stated and not the 2-6-derivative of ordinary phenolphthalein.

I wish to thank Mr. F. J. Taylor for making a number of the phenolic substances used in this investigation.

NOTES ON THE HABITS AND LIFE HISTORIES OF SOUTH AFRICAN ANURA WITH DESCRIPTIONS OF THE TADPOLES.

By J. H. Power.

(With nine Text-figures.)

Thanks to the Research Grant Board the writer was able to pay another visit to Lobatsi, B.P., during January 1926. On this occasion as on the previous one several important observations were made, some of which are recorded here ; accounts of others will appear in due course.

Phrynobatrachus natalensis, Smith.

This little frog has a wide distribution, being recorded from as far north as Lake Chad, while within the Union it is known to occur in the Transvaal, Natal, Orange Free State, and Cape Province.

It is not strictly nocturnal for the author has heard it calling throughout the day at Lobatsi, B.P. It is, however, more active at night when it hops about in search of ants and other small insects on which it feeds.

The call of the male resembles that of *Bufo regularis*, but is not nearly so loud ; it consists of a repeated *waap, waap, waap.* The female is grasped in the axillary region and the pair swim about until the eggs are expelled.

Eggs to the number of between 800 and 1000 are disposed in a more or less circular patch about 3 ins. in diameter. They float in a single layer each surrounded by a perfectly transparent sphere of mucilaginous jelly, which renders them quite inconspicuous. The dark upper poles of the eggs hardly show against the decaying vegetable matter at the bottom of a clear pool ; this added to their very small size, ·5 mm. in diameter, makes it a difficult matter to find them.

Notwithstanding that the transparent capsules adhere to each other it is difficult to collect a whole patch as some are likely to become detached. The writer found that the easiest and surest way is to allow it to float with the inrush of water into a tin submerged beside it.

Eggs that were laid on the night of 15th December measured ·5 mm. in diameter.

On 21st December they measured, total length 3 mm., tail 2 mm.

External gills visible as short branches at either side of the head; eyes indicated by two brown spots; adhesive apparatus visible.

22nd December, total length 3·5 mm., tail 2·5 mm. Eyes with pupil forming; left gill still visible, right one almost disappeared.

23rd December, total length 4·5 mm., tail 3 mm. Mouth parts beginning to form, spiraculum just visible microscopically; gut shows signs of forming.

24th December, total length 5 mm., tail 3·5 mm. Gut fairly well formed, but no sign of food yet; tadpoles now beginning to show a slight transparent brown colour.

25th December, total length 5 mm., tail 3 mm. Gut at this stage contains food; anus apparently median.

27th December, total length 6 mm., tail 4 mm. Mouth parts at this stage as in fig. 1.

FIG. 1.—Mouth disk of *Phrynobatrachus natalensis*. Twelve days old.

30th December, total length 7 mm., tail 4 mm. Mouth parts now fully developed.

11th January, total length 12 mm., tail 7 mm. The legs begin to appear.

16th February, total length 20 mm., tail 13 mm. This is the greatest length reached.

30th March, total length 19 mm., tail 11 mm. The arms come through, first the left.

On 8th April the tiny frogs measuring 8 mm. finally leave the water. The tail is almost completely absorbed. Thus the metamorphosis has taken 114 days to complete.

Length of body once and one-third the width; nearly two-thirds the length of the tail. Nostrils nearer the eye than the end of the snout. Eyes

FIG. 2.—Tadpole of *Phrynobatrachus natalensis*, from Lobatsi, B.P.

on the upper surface; nearer the end of the snout than the spiraculum, the distance between them slightly greater than the distance between the nostrils; much less than the width of the mouth.

Spiraculum on the left side, directed upwards and backwards; nearer to the posterior end of the body than to the eye; visible from above and below.

Anal tube horizontal, opening on the lower edge of the sub-caudal fin, but bent over to the right.

Tail three and two-third times as long as deep ; obtusely pointed ; upper crest convex, originating just in front of the vertical through the origin of the legs ; more than twice as deep as the lower, which is almost straight ; the depth of the muscular portion at the base about half the greatest total depth.

The mouth disk (fig. 3) of this species is small and distinctly transverse ; the upper lip nearly straight and edged with very small horny teeth ; the lower lip and sides edged with rather blunt papillae ; a distinct inward fold at the sides. The upper beak is very wide and shallow ; both upper and lower beaks minutely denticulate and narrowly edged with black ; the middle part of the upper almost straight. There are two rows of horny teeth on the lower lip ; the inner row reaching the full width of the mouth and broadly interrupted in the centre ; the outer row very short and uninterrupted. The dental formula is $\frac{1}{2}$.

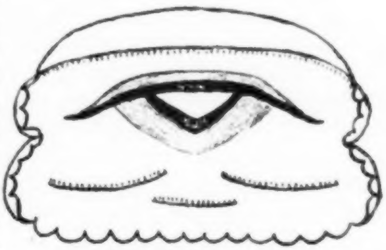


FIG. 3.—Mouth disk of *Phrynobatrachus natalensis*, full grown, from Lobatsi, B.P. Much enlarged.

Colour.—The colour in life is greyish above, transparent below. In very young tadpoles both dorsal and ventral surfaces are transparent. The grey colour in the adult tadpoles is so like the leaves and other decaying vegetable matter that it is very difficult to distinguish them as they lie motionless on the bottom. The tail is spotted all over with dark brown.

Rana fuscigula, Dum. and Bibr.

This is the commonest species of the genus *Rana* in South Africa, being widely distributed over the interior. The British Museum Catalogue records it from Sierra Leone and West Africa, and the Kimberley Museum has a specimen from Penhalonga, Southern Rhodesia. It is the common form of Western Cape Province, extending eastward along the coast to at least Mossel Bay. The common frog of the Transvaal seems to be *Rana angolensis*. Those two species are so very much alike that there seems to be some confusion as to their limits.

Rana fuscigula is an aquatic frog, being seldom found far away from water. In the Kimberley district it lives in dams of clear water and in running streams. The croaking of the males may be heard practically the whole

year round, but the continuous loud *rat-tat-tat-tat* is heard only during the breeding season, which is from September to the end of May.

The males usually sit in the water near the edge, calling as above. Breeding takes place at night; the female is grasped under the arms, the hands of the male almost meeting in front.

The eggs are small (1·5 mm. in diameter), are laid singly and attached to weeds. This is an interesting fact, for in every other known species of *Rana* the eggs are laid in a mass. Nearly 900 eggs were laid in a petrol tin by the female of a pair taken in embrace on the night of 19th April. On the following night an additional 1080 were laid. All these were laid probably in the excitement of confinement.

The metamorphosis varies from about three months to a seemingly indefinite period. The writer has known tadpoles to remain as such for three years. The cause of this retardation of the metamorphosis is unknown. It certainly is not a matter of either temperature or confinement, for the writer has found tadpoles which, judging by their size (6 ins. or more), were more than three years old, in places eminently suited to metamorphosis. Moreover, such giant tadpoles may be collected in running streams the whole year round.

The following account is of a metamorphosis which was gone through in a petrol tin cut longitudinally :—

Eggs collected on 6th October at a marked spot, where pairs were seen in embrace, measured 1·5 mm., the capsule being 3·5 mm.

10th October, embryo measured 2 mm.; the tail had begun to develop.

14th October, total length 4 mm., tail 1·5 mm.; they were still in the egg-capsule; the eyes visible as tiny dark spots; the adhesive apparatus visible; the egg-capsule measured 5 mm.

16th October, total length 5 mm., tail 3 mm.; they left the egg-capsule on this date; the labial papillae and the beginning of the mouth were visible; the external gills showed as two very small groups of finger-like protuberances on either side.

18th October, total length 6 mm., tail 4 mm. Only the tips of the fast-disappearing gills were visible, they were evidently fully developed before the larvae left the egg-capsule.

21st October, total length 9 mm., tail 5 mm.; the external gills had completely disappeared; the mouth, eyes, and spiral gut plainly visible to the naked eye; the spiraculum could be seen by the aid of a high-power lens; the gut showed signs of food.

26th October, total length 11 mm., tail 7 mm.; the ventral surface had begun to lose its transparency, opaque metallic white appearing first over the gut and gradually spreading towards the mouth until by 1st December it had spread over the whole ventral surface.

9th November, total length 50 mm., tail 34 mm.; the legs began to appear.

1st December, total length 68 mm., tail 39 mm. This was the greatest length reached; the legs were then well developed and the hands visible beneath the skin.

6th December, total length 66 mm., tail 38 mm. The hands, first the left, through the spiracular opening, came through on this date.

10th December, the tailed frogs began to leave the water. The tail now became gradually absorbed until on 26th December it had entirely disappeared.

The metamorphosis in this case took 81 days. It may be added that the weather was unusually warm during the above-mentioned period, the temperature of the water scarcely ever going below 25° C., often reaching 40° C. The average during the day, throughout the period of metamorphosis, was 37° C.

Length of body slightly more than twice its width, considerably more than half the length of the tail. Nostrils about midway between the eyes

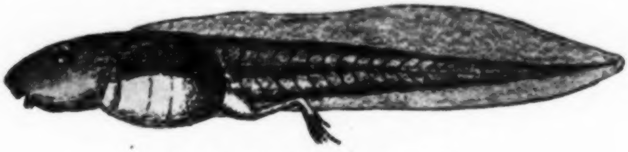


FIG. 4.—Tadpole of *Rana fuscigula.*

and the end of the snout. Eyes on the upper surface of the head, equidistant from the end of the snout and the spiraculum; the distance between them more than twice the distance between the nostrils; greater than the width of the mouth.

Spiracular opening rather small (even in tadpoles 4·8 inches long it was only a millimetre in diameter), on the left side, directed mostly upwards and backwards; slightly nearer the end of the snout than the anus; just visible from above.

Anal opening on the lower edge of the sub-caudal fin; bent over to the right.

Tail more than three times as long as deep; upper crest not convex and about twice the depth of the lower; extending about one-third the length of the back; the muscular portion at its base less than two-thirds the total depth.

Beak (fig. 5) broadly edged with black; sides and lower edge of the lip bordered with papillae in a single row except at the sides. Upper lip with a series of fine teeth followed on either side by three or four series which are

broadly interrupted in the centre and gradually diminishing in length towards the centre of the mouth; three or four series of teeth on the lower lip, the first short, the second and third extending the full width of the mouth; the third interrupted in the centre. The series may be represented by the formulae $\frac{4}{3}$ or $\frac{5}{4}$.

Colour.—The colour in life is olive above, speckled and marbled by minute darker spots, the sides have a metallic golden tinge with dark olive speckles and the undersurface mother-of-pearl white. Tail greyish, closely spotted with grey or dark brown, the muscular portion having comparatively large blotches on the top. In young specimens, before the legs have developed much, the upper surface of the body and tail have a general greyish tinge

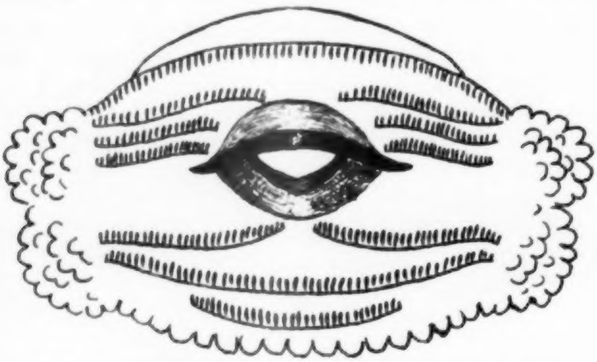


FIG. 5.—Mouth disk of *Rana fuscigula*, full grown. Much enlarged.

resembling the sandy bottoms of the streams where they are found, but as they grow older the colour deepens to a dark olive.

Habits.—They seem to spend practically all their time, at least during the day, resting on the bottom. If they do move towards the surface, as soon as they cease swimming they at once sink to the bottom like a stone. You may watch them for hours at a time without their showing signs of life.

Rana oxyrhynchus, Smith.

This frog inhabits both muddy pools and clear streams of running water. It is seldom met with in the daytime as it hides away in holes and under stones, but during the night, in the breeding season, the males in particular are very plentiful wherever water is to be found.

Breeding takes place only at night, the males sit away from the water's edge and call for a mate. The sound made is a continuous *kreck, kreck, kreck*. When a number of males are calling together at one pool an indi-

vidual occasionally breaks into a very quick repetition of the call, resembling very much the noise made by a Kiewitje (*stephanibyx cornatus*), when disturbed. It was thought that this agitated call was caused by a responsive note from a female, but no definite observation on the subject was made.

The call is produced by inflating and deflating the vocal sacs with each emission of sound. The vocal sacs are internal and are a dark shiny colour when fully inflated.

The male grasps the female in the axillary region and the pair do not enter the water until the female is ready to lay the eggs. There seems to be no partiality in the choice of a site as the writer has found eggs in muddy pools and also in clear ones.

Eggs of this species were laid in a muddy pool at Lobatsi in the early morning of 10th January 1926. They were attached to one another, in short strings varying from three to eight inches, by a very thin web-like strand and floated on the surface. Evidently they eventually become separated, for several single eggs were collected floating about. The egg-capsule is very mucilaginous and soon becomes coated with all sorts of foreign matter, which may come in contact with it as it floats about. In this way it becomes effectually disguised and difficult to find, more especially if there are flower-bearing acacias near at hand, the flowers of which, when in the water for some time, look exactly similar to the disguised eggs of *Rana oxyrhynchus*.

Several eggs were collected and transferred to an aquarium; the outer capsule measured 3 mm., the vitelline egg 1·0 mm. The upper half of the egg is dark brown, the lower half whitish.

On 10th January (afternoon) the embryos had begun to develop, some being 2 mm. long and showing the beginning of the tail.

11th January (morning), total length 2·5 mm., tail 5 mm.

11th January (afternoon), still in capsule which had swollen to 4 mm. Total length 3·5 mm., tail 1·5 mm. The adhesive apparatus was prominent, and the external gills had begun to form.

12th January (morning), they had left the egg-capsule. They then measured 5 mm., tail 3 mm. External gills fully developed, and two tiny black spots indicating the position of the eyes were visible.

15th January, total length 8 mm., tail 5 mm. Spiracular opening visible for the first time. The external gills had entirely disappeared.

26th January, total length 18 mm., tail 11 mm. Legs began to appear.

15th March, total length 31 mm., tail 19 mm. A violent hailstorm on the afternoon of the above date filled the development tanks and destroyed all the tadpoles. The legs had developed to a considerable extent, but the arms had not come through.

Length of body more than once and a half its width, about two-thirds

the length of the tail. Nostrils about half-way between the eye and the end of the snout; eyes on the upper surface of the head somewhat nearer to the end of the snout than to the spiraculum; the distance between them

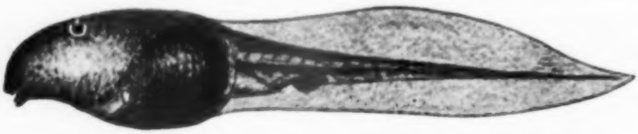


Fig. 6.—Full-grown Tadpole of *Rana oxyrhynchus*. Much enlarged.

twice to twice and a half as great as that between the nostrils, about equal to or slightly greater than the width of the mouth.

Spiraculum very low down on the left side, directed upwards and backwards; about midway between the anus and the end of the snout; visible from below, not visible from above.

Anus median, opening on the lower edge of the sub-caudal crest. Tail nearly four times as long as deep, acutely pointed, upper crest convex, once and a half as deep as the lower, not extending on the back; the depth of the muscular portion at the base slightly more than half the total depth.

Beak (fig. 7) fairly deeply edged with black, sides and lower edge of the lip bordered with papillae usually in two rows; upper lip with a long series

Fig. 7.—Mouth disk of *Rana oxyrhynchus*. Much enlarged.

of fine teeth, two series of teeth on the lower lip, the outer of which may be straight or very much bent in the centre, the inner is broadly interrupted in the centre or broken into three or more small strips.

Colour.—Ashy-grey or greyish olive above the head, covered with minute silvery or pale golden spots except the front from the level of the eyes, which is transparent. Sides speckled with brown; belly pale golden-yellow;

throat transparent. Tail greyish or olive, upper fin spotted with brown, lower fin transparent.

Bufo regularis, Reuss.

This is the commonest species of the genus *Bufo* found in South Africa. It is distributed over the whole continent from the Cape to the Mediterranean Sea, with the exception of Barbary.

It was thought to be absent from the Cameroon-Gaboon area, but several records have been published from that region within recent years.

Such an extensive distribution with its attendant wide range of climatic conditions has given rise to numerous local forms which, however, are difficult to define sharply.

It is not as common as *Bufo carens* at Lobatsi, B.P., but is fairly plentiful there. Both species were found breeding in the same pool not only with their own kind but males of *Bufo regularis* with females of *Bufo carens* and vice versa. Owing to the numbers of breeding pairs in the above-mentioned pool the writer was unable to obtain the eggs from such crosses.

The call, mode of embrace, etc., of this species has already been described.* The following account of the metamorphosis has been drawn up from observations made at Kimberley :—

The eggs are rather small, measuring only 1·0 mm. in diameter, black above, the lower pole being whitish, approximately 23,000 are laid by the average adult female. They are enclosed in two tubes of jelly-like substance ; in newly laid eggs these tubes measure 2 mm. in diameter.

At noon on 4th November 1925 three pairs were observed in embrace at Kenilworth Dam, near Kimberley, while two unpaired males were calling lustily. They had been calling since sundown the previous evening. Egg-laying was in progress and several strings were to be seen coiled among the weeds where the toads were. It was noticed that all the males were somewhat smaller than the females, the characteristic markings on both sexes being clearer and more brilliant than is usual in specimens from the Kimberley neighbourhood. A large number of eggs were taken from a batch which had just been laid and put in a small aquarium.

On the morning of 6th November the outer tubular capsule had swollen to 3 mm., each inner capsule being 2 mm. and the embryos 1·5 mm. (The outer capsule may swell to 4 or 5 mm. in diameter if the eggs become irregularly distributed inside.) At this stage the outer capsule was ruptured and the embryos, surrounded by the inner circular capsule, floated out, but still adhered to each other and to the gelatinous tube. At noon on 6th November the more advanced embryos were 2·5 mm. long with the adhesive apparatus visible to the naked eye. They were still within the egg-capsule,

* Trans. Royal Soc. S. Afr., iii, p. 173, 1913.

which was very much swollen, the position of the eyes was marked by tiny black spots. On the same day at six p.m. the embryos had left the capsule and were suspended from it by the adhesive apparatus. They measured 4·5 mm.; a tiny tail ·5 mm. long had developed.

On 7th November the more advanced ones measured 6 mm., tail 2·5 mm. The appearance of the adhesive apparatus at this stage was like that of an irregular pit; the external gills were now beginning to make their appearance.

On 8th November, total length 6 mm., tail 3 mm. The external gills were much developed, and myriads of minute lamellae surrounded the adhesive apparatus.

On 9th November, total length 6·5 mm., tail 3·5 mm. External gills very large and branching and quite visible to the naked eye. Body black, tail-fin grey.

On 10th November, total length 7 mm., tail 4·5 mm. The external gills were still fairly prominent though there were signs of their beginning to shrink. At this stage the gut was beginning to form.

On 11th November, total length 8 mm., tail 5 mm. The right gill had completely disappeared, the left was still projecting considerably. The gut, the beak, and the eyes were formed; the rows of horny teeth were beginning to show; the adhesive apparatus was still visible.

On 12th November, total length 9 mm., tail 5 mm. The external gills had completely disappeared; the spiraculum was visible on the left side; the gut showed signs of food, the anus was open on the median line; the horny teeth were visible; the adhesive apparatus had almost disappeared.

On 18th November, total length 13 mm., tail 8 mm. At this stage the legs began to appear.

On 28th December they reached their greatest length; they then measured total length 25 mm., tail 14·5 mm. From this time onwards they showed a disposition to rest on the bottom of the tank, the characteristic colour markings began to show, and on 10th January the arms, first the left, came through; the tail at this stage measured 13 mm.

The tailed toads now rested continuously in very shallow water with the nostrils above the surface. On 12th January they showed a disposition to leave the water, the tail then being about two-thirds absorbed. By 16th January they had entirely abandoned the water and the tail was completely absorbed. The metamorphosis, thus taking 73 days to complete, is in striking contrast to that of *Bufo vertebralis*, which takes only 16 days.

Length of body somewhat more than once and a half its width; about three-fourths the length of the tail. Nostrils much nearer the eye than the end of the snout. Eyes on the upper surface of the head much closer to the snout than to the spiracular opening, the distance between them

twice that between the nostrils; about equal to or slightly less than the width of the mouth.

Spiraculum low down on the left side, but visible from above; directed slightly upwards and backwards; equidistant from the anus and the end of the snout or slightly nearer the former, opening equal to that of the anus.

FIG. 8.—Full-grown Tadpole of *Bufo regularis*. Much enlarged.

Anus median, directed backwards, opening on the lower edge of the sub-caudal fin.

Upper tail-crest but very slightly convex, not extending on to the back, beginning just above the origin of the legs; equal in depth to the lower. Lower tail-crest almost straight.

Tail less than three times as long as deep, obtusely rounded at the end; depth of muscular portion at its base about half the greatest total depth.

Beak (fig. 9) broadly edged with black. Sides of the mouth bordered with papillae in one row. Upper lip with a long series of horny teeth followed by a shorter series which is broadly interrupted in the centre. Three series of teeth on the lower lip, the first and third continuous, the second narrowly interrupted in the centre, the outermost the shortest and bordering the lip.

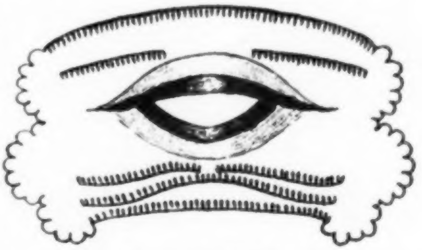


FIG. 9.—Mouth disk of *Bufo regularis*. Much enlarged.

Colour.—The colour is jet black except the tail-fins, the upper of which is transparent with minute black spots and wavy lines, while the lower is transparent. It was noticed that the dark chromatophores on the head contracted at night into sub-spherical masses making the colour almost transparent instead of black.

Habits.—These tadpoles do not assemble in masses, nor are they so active as in the case of *Bufo carens*, but lead more or less an independent life. It was observed that when a dead frog or tadpole was placed in the aquarium the *Bufo regularis* tadpoles became very agitated, and swam almost directly to the dead animals, thus exhibiting a keen sense of smell.

SOME TADPOLES FROM GRIQUALAND WEST.

By J. H. Power.

(With Plate XV.)

Cacosternum boettgeri, Boulenger.

The systematic position of this frog has given herpetologists much trouble since it was first described. Even at present, forty years after it was discovered, its relationship to the various genera is by no means clear. It was originally described by Boulenger as a species of *Arthroleptis* (belonging to the *Ranidae*) (1), but afterwards the author referred it to the genus *Cacosternum* (*Engystomatidae*) (2); later, Hewitt (3), on the discovery of teeth in the upper jaw, placed it in the sub-family *Dyscophinae* (4).

The discovery of that remarkable frog *Anhydrophryne* again, because of their affinities, brought *Cacosternum* to the fore. Warren (5), in the summary of his work on the development of the tadpole of *Anhydrophryne*, says: "Hewitt refers *Anhydrophryne*, which has a toothed upper jaw, to the *Ranidae*, and in some respects it resembles the genus *Cacosternum*, which is also toothed, and perhaps should be regarded as a Ranid." Further on he says, "In the embryo of *Anhydrophryne* the sacral diapophyses are large and almost cylindrical and Ranid in character." The present writer finds that the above also holds good for the tadpoles of *Cacosternum*.

Hewitt (6), in 1919, says: "Again, the pectoral girdle of the toothed genera Anhydrophryne and Cacosternum very closely resembles that of the toothless Engystomatid genus Phrynomantis, but this has greatly enlarged sacral diapophyses, like Cacosternum." Further down he says: "From the above-mentioned facts it will be understood that the supposed relationship between Phrynomantis, Cacosternum, and Anhydrophryne is an inference based solely on the characters of the pectoral girdle, due allowance being made for the fact that these three genera are South African, the two latter being peculiar to the continent." It appears now that all three genera are peculiar to South Africa (see Noble, May 1926, (7)), the Amboyna species being now proved to belong to a distinct genus. The above author proposes the name *Phrynomerus* for the South African species.

Again, Noble, in 1922 (8), says: "The relationships of *Phrynomantis*

to *Anhydrophryne* and *Cacosternum* suggest that the Breviceptidae are but toothless dyscophids."

Now the question arises, can a study of the tadpole throw any light on the matter?

Fortunately, the highly specialised larva of *Phrynomerus* (see Power, 1926, (9)) has the same general characteristics as those of the Indian Engystomatids, *Microhyla* and *Calluella*, thus bearing evidence to their relationship. On the other hand, the larva of *Cacosternum*, here figured and described for the first time, shows no specialisation whatever. The rows of horny teeth show a considerable amount of variation, there being occasionally a short row bordering the lower lip as in the case of the genus *Bufo*. The spiraculum is directed straight backwards as in the genus *Bufo*, and the position of the anus as in the larva of *Cassina* (see Power, 1926, (9)). From the above it would appear that *Cacosternum* has Bufonid affinities.

Tadpole (fig. 1, Pl. XV).—Total length, 33 mm.

Body.—Length of body one and five-seventh times its width, about three-fifths the length of the tail; nostril slightly nearer the eye than the end of the snout; eyes on the upper surface, slightly nearer the end of the snout than the spiraculum, the distance between them * about four times the distance between the nostrils, greater than the width of the mouth.

Spiraculum.—Spiracular opening very small, difficult to distinguish in living specimens, low down on the left side, directed but slightly upwards and backwards, often perfectly horizontal, slightly nearer the posterior end of the body, visible from below, not visible from above.

Anus.—Anal opening on the right of the median line above the edge of the sub-caudal fin and beneath the origin of the right leg, the opening directed almost vertically downwards, about equal to or slightly larger than the spiraculum.

Tail.—Tail three and a half times as long as deep, pointed, upper crest very slightly convex; the depth of the muscular portion at its base half the total depth.

Mouth (fig. 1*a*, Pl. XV).—Beak white, edged with black; lips bordered by a single row of papillae, broadly interrupted above where the lip is toothed.† The anterior series of teeth is followed by two or three others

* From the anterior corner of the one to that of the other.

† The series of teeth are subject to considerable variation; an examination of twenty specimens taken from the same pool gave the following results:—

$$\dfrac{\dfrac{1}{2-3}}{[illegible]},\ \dfrac{\dfrac{1}{2-2}}{3},\ \dfrac{\dfrac{1}{3-2}}{4},\ \dfrac{\dfrac{1}{2-2}}{3},\ \dfrac{\dfrac{1}{2-2}}{3},\ \dfrac{\dfrac{1}{2-2}}{3},\ \dfrac{\dfrac{1}{3-3}}{4},\ \dfrac{\dfrac{1}{3-3}}{3},\ \dfrac{\dfrac{1}{2-3}}{3},\ \dfrac{\dfrac{1}{2-2}}{3},$$

$$\dfrac{\dfrac{1}{2-2}}{3},\ \dfrac{\dfrac{1}{2-2}}{3},\ \dfrac{\dfrac{1}{2-2}}{3},\ \dfrac{\dfrac{1}{3-3}}{3},\ \dfrac{\dfrac{1}{2-2}}{3},\ \dfrac{\dfrac{1}{2-3}}{3},\ \dfrac{\dfrac{1}{2-2}}{3},\ \dfrac{\dfrac{1}{2-2}}{3},\ \dfrac{\dfrac{1}{2-2}}{3},\ \dfrac{\dfrac{1}{2-2}}{3}.$$

which are broadly interrupted in the middle and gradually decrease in length, the fourth series, if present, being extremely short. On the lower lip are three series all extending the full width of the mouth, the first two being close together and near the edge of the lower lip, the third is close up to the horny beak and is curved up abruptly to form a point in the centre. There is, occasionally, a fourth short row bordering the centre of the lower lip as in the genus ***Bufo***.

The formula $\frac{1}{\frac{2-2}{3}}$ represents the more usual occurrence found in the series.

Colour.—The colour in life is semi-transparent, yellowish olive, light brown, or dark grey above; opaque white beneath, with usually a bright metallic lustre. The muscular tail may be plain yellowish or spotted with brown; tail fins transparent. Tadpoles taken in muddy pools are, as a rule, light grey or yellowish above; those kept in an aquarium where the water is clear are dark grey or dark brown above. When the hands break through, the tadpoles exhibit all the variety of markings observed in the adults.

Habits.—As these tadpoles live almost exclusively in muddy pools, it is rather difficult to study their habits. As far as the writer is aware they do not assemble and swim in colonies, but rest on the bottom as in the case of ***Pyxicephalus delalandi***.

Pyxicephalus delalandi, Tschudi.

Tadpole (fig. 2, Pl. XV).—Total length, 39 mm.

Body.—Length of body a little more than one and a half times its width, somewhat more than two-thirds the length of the tail. Nostrils a little nearer the eye than the end of the snout. Eyes on the upper surface equidistant from the end of the snout and the spiraculum; the distance between them about two and a half times the distance between the nostrils, greater than the width of the mouth.

Spiraculum.—Spiraculum rather low down on the left side, directed upwards and backwards, equidistant from either extremity of the body, barely visible from above, quite distinct from below.

Anus.—Anal opening median, slightly larger than the spiraculum and close to the body.

Tail.—Tail more than three times as long as deep, rounded at the end; both crests slightly convex, the upper one about one and a half times as deep as the lower one; not extending upon the back, the depth of the muscular portion at its base about half the total depth.

Mouth (fig. 2*a*, Pl. XV).—Beak white, edged with black; lips bordered with one row of papillae, below and at the sides, broadly interrupted above

by a toothed edge, followed by two other series broadly interrupted in the middle and decreasing in length. On the lower lip is a short outer series followed by two others which extend the full width of the mouth, the innermost one being slightly interrupted in the centre. The series being represented by the formula $\frac{3}{3}$.

Colour.—They usually take the colour of the mud or sand on the bottom of the pool. This, coupled with the fact that they spend the major portion of their time on the bottom, makes them very difficult to see. In fact it is quite impossible to see them even in clear water unless they move. The ventral surface is very transparent, the spiral gut being quite visible. The part behind the mouth is a deep pink.

Habits.—Each individual leads an independent existence; the writer has, however, seen groups of tadpoles of this species together. They remain mostly at the bottom of the pool, feeding on minute water plants there, but may also be seen at the sides.

Pyxicephalus adspersus, Tschudi.

Tadpole (fig. 3, Pl. XV).—Total length, 71 mm.

Body.—Length of body one and five-eighth times the width, about seven-elevenths the length of the tail. Eyes on the upper surface, the distance between them about twice the distance between the nostrils; about equal to the width of the mouth.

Spiraculum.—Spiracular opening low down on the left side, directed upwards and backwards, slightly nearer to the snout than the vent.

Anus.—Anal opening on the lower edge of the sub-caudal fin and bent over to the right, larger than the spiraculum.

Tail.—Tail about three and one-third times as long as deep, rounded at the end; upper crest but very feebly convex, lower crest almost straight; the former not extending on the back and almost the same depth as the lower one, the depth of the muscular part at its base slightly less than half the total depth.

Mouth (fig. 3*a*, Pl. XV).—Beak white, deeply edged with black; lips bordered by a single series of papillae, except at the sides where the series is doubled, broadly interrupted in the middle of the upper lip, a well-marked chink on either side of the lower lip. Series of labial teeth $\frac{4}{3}$; the first and second on the upper lip extending the full width of the mouth, the third and fourth broadly interrupted in the centre by the beak, the three lower series occupying the whole width of the lip.

In general appearance and build this tadpole is exactly similar to *Pyxicephalus delalandi*. Unfortunately I have not been able to study it in life. The above account being written from spirit specimens.

Bufo vertebralis, Smith.

Tadpole (fig. 4, Pl. XV).—Total length, 16 mm.

Body.—Length of body about one and three-eighth times the width, slightly more than three-fifths the length of the tail. Nostrils much nearer the eye than the end of the snout. Eyes on the upper surface, the distance between them slightly more than twice the distance between the nostrils; about equal to the width of the mouth.

Spiraculum.—Spiraculum on the left side, directed backwards and slightly upwards, nearer the snout than the anus, rather indistinct but visible from above and below.

Anus.—Anus median, opening on the lower edge of the sub-caudal fin.

Tail.—Tail nearly three times as long as deep, broadly rounded, and turned up slightly at the end; upper crest slightly deeper than the lower and distinctly convex, the lower almost straight; the depth of the muscular portion at its base less than half the greatest total depth.

Mouth (fig. 4*a*, Pl. XV).—Beak white, narrowly edged with black; lips with papillae only at the sides which form an inward fold, both upper and lower edges toothed, the series of teeth being $\frac{2}{3}$; the second upper series as long as the first but broadly interrupted in the centre, the first and second lower series uninterrupted and occupying the whole width of the mouth. The third series interrupted in the centre.

Colour.—The colour above is grey or olive with a dark stripe on either side at the origin of the tail. The light vertebral spot at the apex of a Λ-shaped dark mark, so characteristic of the adult, is present. They are transparent beneath.

Habits.—The tadpoles never move in colonies. They seem to feed mostly on the slime and mud at the bottom of the pool where they are found.

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5. Warren.—S. Afr. Journ. of Sc., xix, p. 261.
6. Hewitt.—Rec. Alb. Mus., iii, No. 3, p. 186.
7. Noble.—Amer. Mus. Nov., No. 212, p. 19.
8. Noble.—Bull. Amer. Mus. N. H., xlvi, p. 19.
9. Power.—Trans. Roy. Soc. S. Afr., xiii, pp. 114–5.

EXPLANATION OF PLATE.

Cacosternum boettgeri, Bouleng.

Fig. 1. Tadpole, about $3\frac{3}{4}$ natural size.
Fig. 1*a*. Mouth-disk of tadpole, ×17.

Pyxicephalus delalandi, Tschudi.

Fig. 2. Tadpole, about $2\frac{1}{3}$ natural size.
Fig. 2*a*. Mouth-disk of tadpole, ×14.

Pyxicephalus adspersus, Tschudi.

Fig. 3. Tadpole, about $1\frac{1}{3}$ natural size.
Fig. 3*a*. Mouth-disk of tadpole, ×12.

Bufo vertebralis, Smith.

Fig. 4. Tadpole, about $2\frac{2}{3}$ natural size.
Fig. 4*a*. Mouth-disk of tadpole, ×43.

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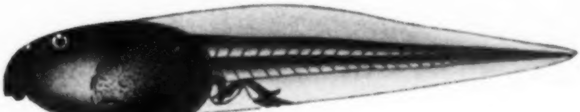

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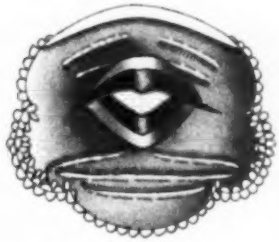

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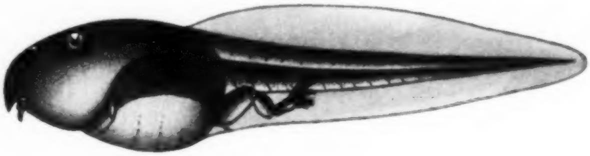

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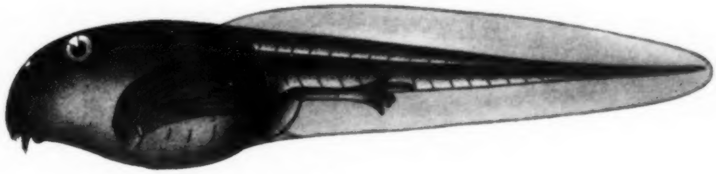

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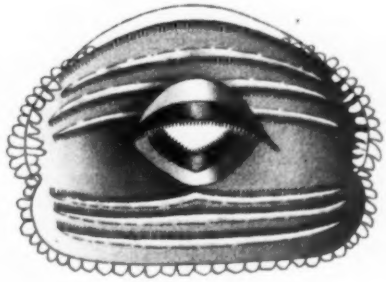

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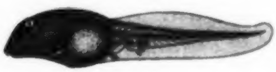

4

J. H. Power, del.

THE NATURE OF THE CO-ENZYME OF LIPASE.

By Louis Pierre Bosman.

(From the Department of Bio-chemistry, University of Capetown.)

A series of experiments, extending over a long period, were first made with the object of ascertaining which would be the most suitable extract of pancreatic lipase and the ester most suitable for hydrolysis. Sheep's and pig's pancreas were tried with olive oil emulsion, diluted cream, methyl acetate, and ethyl butyrate. The best results were obtained with a dilute sodium carbonate extract of sheep's pancreas and ethyl butyrate.

In the vast majority of cases cited below an alkaline extract of the sheep's pancreas was made as recommended by J. Mellanby and V. J. Woolley, viz. the pancreas was carefully freed from fat, finely minced and ground up, and extracted with twice its weight of 0·5 per cent. of sodium carbonate for 24 hours. The mixture was shaken vigorously at regular intervals. The tissue was carefully removed with well-washed muslin. To this extract was added a few drops of chloroform, and it was allowed to stand in a closed bottle for a further 48–72 hours.

The extract was first examined as to the time during which the lipase reached its maximum activity. Variations as to the condition of the pancreas, of course, allow only of an approximation. Generally 3–4 days was sufficient. To quote a case in point: it was found that 2 c.c. of the extract, 24 hours after extraction, hydrolysed 1 c.c. ethyl butyrate in the presence of 5 c.c. water to the extent of 4·16 c.c. N/10NaOH. After 2 days this increased to 4·6 c.c. N/10NaOH, and 4·65 c.c. N/10NaOH after 3 days. No significant increase in this or other cases was observed on the fourth and subsequent days.

Having now arrived at an idea as to extent of the hydrolysis of ethyl butyrate brought about by an extract prepared as above, the effect of dialysing the extract was next investigated.

Fifty c.c. of the extract was dialysed against 200 c.c. distilled water in a parchment thimble for 3 days. The lipolytic power of the original extract, the "inside" liquid, and the dialysate were determined separately. The lipolytic power of a combination of the dialysate and the "inside" liquid was then found. These figures, after allowing for controls, were compared.

The quantity of the original extract was 2 c.c., the effect of which was tried on 1 c.c. ethyl butyrate in the presence of 5 c.c. water. The incubation in each case was carried on for 4 hours at a temperature of 38–40° C.

In other experiments the time of incubation was altered, but the ultimate result was not materially affected. Invariably it was found that the "inside" liquid measured 65 c.c. and the dialysate 185 c.c. The necessary corrections for the quantities of the reacting liquids were made.

The nine cases tabulated below form but a small part of the actual number of experiments carried out. They are significant enough, however, to show that some active substance or substances dialyse out. The figures represent the number of c.c.'s N/10NaOH required to neutralise the acid liberated on hydrolysis of the ethyl butyrate.

No.	Original Extract.	"Inside" Liquid.	Dialysate.	"Inside" Liquid + Dialysate.
1	5·2	3·0	0·1	4·9
2	4·6	2·8	0·1	4·1
3	5·0	2·8	0·2	4·6
4	5·2	2·6	0·3	4·9
5	5·3	2·4	0·2	5·1
6	5·1	2·5	0·2	5·0
7	4·0	2·5	0·2	3·6
8	5·3	2·4	0·3	5·2
9	3·8	1·1	0·1	3·6

The three outstanding facts about the above figures are :

(1) The lipolytic power of the extract was practically halved by being dialysed. In some cases the fall was even greater.

(2) The dialysate showed only a small hydrolysis.

(3) A combination of the "inside" liquid with the dialysate restores approximately the whole of the original degree of hydrolysis.

The lipolytic power of the dialysate did not increase after 8, 16, and 32 hours incubation. Assuming, then, that a co-enzyme of some form dialyses through and that it is responsible for about 50 per cent. of the hydrolysis, the question as to its nature was next considered.

Fifty c.c. of the dialysate was boiled for 10 minutes so as to destroy any true enzymatic substance. The cooled liquid was made up to the original volume, and tested both by itself and in conjunction with the "inside" liquid.

In this particular instance the original extract, the "inside" liquid, and the dialysate showed an hydrolysis of 5·3 c.c., 2·3 c.c., and 0·3 c.c.

N/10NaOH respectively. After the boiling the dialysate and the "inside combined yielded an hydrolysis of 5·2 c.c. N/10NaOH. It would appear that the co-enzyme is probably not truly enzymatic in nature. Further, no results were obtained on trying to extract with ether or on precipitating with absolute alcohol.

140 c.c. dialysate was next taken down to 30 c.c. in vacuo at room temperature. A white substance separated, accompanied by a peptone-like material which imparted to it a slight odour of putrid decomposition. Mellanby and Woolley * also cite the development of a product of proteolytic activity in the dialysed pancreatic juice, owing to the fact that dialysis occupies a considerable time. The same investigators, while giving no evidence as to the nature of the so-called co-enzyme, state, "We are the more inclined to assume that steapsin contained in pancreatic juice cannot be divided into two components corresponding to enzyme and co-enzyme." These authors rightly suggest that the so-called co-enzyme is merely a mixture of inorganic salts which act as activators.

The concentrate of 30 c.c. was now filtered, and the peptone-like material exhibited no lipolytic action. The filtrate, however, retained this property to the same degree as before. Another quantity of dialysate of known volume was taken down to dryness and ashed. On analysis it was found to contain 0·07 per cent. sodium carbonate. That it would contain traces of sodium carbonate was, of course, to be expected, since the extracts were made with 0·5 per cent. sodium carbonate. Then, too, the ash contained 0·065 per cent. of phosphoric oxide, besides traces of sodium chloride.

Three solutions were then prepared, one containing 0·07 per cent. Na_2CO_3, another 0·065 per cent. P_2O_5, and a third containing a mixture of these two in the proportion specified.

The ashed material was made to its original volume and combined with some fresh "inside" liquid, when it was found that the lipolytic power was restored. In this particular case the lipolytic power of the original extract was 4·0 c.c. N/10NaOH. Whereas a combination of the ashed material restored this, the combination of the "inside" liquid with the 0·07 per cent. sodium carbonate solution showed an hydrolysis of only 2·6 c.c. N/10NaOH. So that while the sodium carbonate activated the hydrolysis, it was not to the same extent as that of the solution of the ashed material. The hydrolytic power of the sodium carbonate solution itself is practically zero.

The "inside" liquid was now combined with the mixture of the carbonate and phosphate solutions, and it was found that the original hydrolysis was restored. It appeared, therefore, that a mixture of these two

* Mellanby and Woolley, Journ. Physiol., xlviii, 295.

solutions had the same effect on the "inside" liquid as the dialysate or the solution of the ashed material.

During dialysis an equilibrium is, of course, finally attained. If now we take a greater volume of liquid outside and a smaller volume of extract inside, more of the so-called co-enzyme would dialyse out, and the hydrolytic power of the "inside" liquid would drop. Accordingly 10 c.c. of the extract was dialysed against 300 c.c. distilled water for 3 days. It was found that the hydrolytic power of the "inside" liquid dropped from 2·5 c.c. to 1·1 c.c. N/10NaOH. The 10 c.c. extract had increased from 10 c.c. to 20 c.c. Simultaneously the original "inside" liquid was examined to see whether the fall was not due to loss of activity on standing. It, however, showed an hydrolysis of 2·5 c.c. N/10NaOH. There was, then, no question of deterioration on standing. We notice, therefore, that the hydrolysis was reduced by 50 per cent. by the above procedure.

Dialysing against running water was obviously the next step. Ten c.c. was dialysed against running water for 48 hours. The "inside" liquid increased from 10 c.c. to 20 c.c. as before, and again showed an hydrolysis of 1·1 c.c. N/10NaOH. So that whether we dialyse 10 c.c. against running or 300 c.c. water, the hydrolysis drops from 4·0 c.c. to 1·1 c.c. N/10NaOH —approximately 25 per cent. of the original extract. Dialysis for longer periods against running water did not bring about any further diminution in the degree of hydrolysis. In one case it fell to 0·5 per cent., but as repeated attempts did not yield this result again it cannot be relied upon.

At this stage it was deemed advisable to determine whether the phosphate was a contributary factor to the degree of hydrolysis. The "inside" liquid of a sodium carbonate extract was combined with the dialysate of an aqueous extract. The carbonate extract itself, the "inside" liquid, and the dialysate hydrolysed to the extent of 4·4 c.c., 2·6 c.c., and 0·4 c.c. N/10NaOH respectively, whereas a combination of the "inside" liquid and the dialysate showed an hydrolysis of 4·2 c.c. N/10NaOH. The corresponding figures for the aqueous extract were 3·3 c.c., 1·6 c.c., 0·4 c.c., and 3·0 c.c. N/10NaOH respectively. The "inside" liquid of the carbonate extract combined with the dialysate of the aqueous extract gave on hydrolysis 3·9 c.c. N/10NaOH. We observe that this is slightly lower than the first combination and somewhat higher than the second combination.

In the first case we had the combined effect of the carbonate and the phosphate, and in the second case the effect of the phosphate only—combined, of course, with traces of chloride, carbonate, and other salts which are probably present in the original pancreas. Addition of phosphate to the original extract did not increase the amount of hydrolysis. This indicates that the quantity of phosphate present in the pancreatic extract

is probably the optimum amount. The phosphate in this concentration does not hydrolyse the ethyl butyrate.

Summarised, then, we find that the so-called co-enzyme of lipase is not a definitely true enzymatic substance. It consists of a mixture of inorganic salts which are activators, and that these are sodium carbonate and phosphate. The actual form in which the phosphate is present was not investigated.

The author wishes to thank Prof. E. S. Edie of this University for the interest taken in this work, and also for the helpful advice given to him.

ON A NEW *PHYSALOPTERA* FROM AN EAGLE AND A TRICHOSTRONGYLE FROM THE CANE RAT, WITH NOTES ON *POLYDELPHIS QUADRICORNIS* AND THE GENUS *SPIROSTRONGYLUS*.

By H. O. Mönnig, B.A., Ph.D., B.V.Sc.,
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(With six Text-figures.)

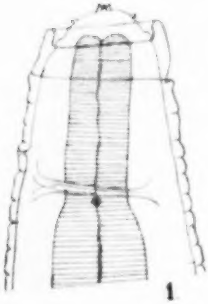
Physaloptera rapacis n. sp.

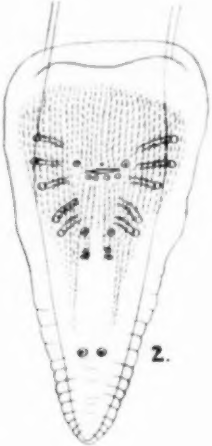
White, moderately short, thick worms. The cuticle has very coarse and deep transverse striations superimposed on other very fine and closely arranged transverse markings. The cuticle is not completely reflected over the lips, but the latter project slightly beyond the head collar. The lips are semicircular and bear each a pair of prominent spherical lateral papillae which project beyond the border of the lip in a lateral view. Each lip bears two terminal teeth, the inner median being higher than the outer and tripartite with the middle tip slightly lower than the others (fig. 1). The cervical papillae are situated at the level of junction of the muscular and glandular parts of the oesophagus, the nerve ring surrounds the muscular portion of the oesophagus slightly in front of this level. The excretory pore is placed at the level of junction of the middle and posterior thirds of the muscular oesophagus. The oesophagus is straight and has muscular and glandular portions which in the female are respectively 0·29 mm. and 3·27 mm. long, or together about 1/4·9 of the body length; in the male the oesophagus is one-fourth of the body length.

The male is 10·6 mm. long and 0·54 mm. thick. The body tapers slightly anteriorly. The caudal alae are large in proportion to the size of the worm and are lanceolate in outline. There are five pairs of pedunculated lateral papillae, of which two pairs are precloacal and the others postcloacal; the first three pairs are equidistant, the last two placed a little further back and well behind the cloacal opening. There are three ventral precloacal papillae, of which the median is very small. The ventral postcloacal papillae are five pairs, of which the first and second pairs are small and situated on the posterior border of the cloaca, the third pair is

situated at the same level as the fifth pair of lateral stalked papillae, the fourth pair is small, shortly pedunculated and placed at the end of the first third of the tail, the fifth pair is large and placed at the end of the second third of the tail. The ventral surface of the caudal alae is ornamented with longitudinal rows of tubercles which do not reach the last pair of ventral papillae (fig. 2). The spicules are short, equal, and measure 290 μ in length.

The female is 17 mm. long and 0·8 mm. thick. The body tapers slightly towards its extremities. The vulva is inconspicuous and opens 0·19 mm.





Physaloptera rapacis.

FIG. 1.—Anterior end, lateral view. FIG. 2.—Tail end of male.

behind the posterior end of the oesophagus. The vagina passes straight back for 0·9 mm., followed by an egg chamber 1·54 mm. long, a common uterine trunk 1·35 mm. long, and two backwardly directed uteri. The eggs are thin-shelled, elongate, and measure 43 $\mu \times 15$ μ. Oviparous.

This species is rather peculiar in possessing five pairs of lateral pedunculated papillae on the male tail instead of the usual four. The combination of its other characteristics, viz. the teeth, the female genitalia, and the male spicules serve to separate it definitely from the other nine species of *Physaloptera* so far known from hawks.

Host.—*Aquila rapax* (Tawny eagle).

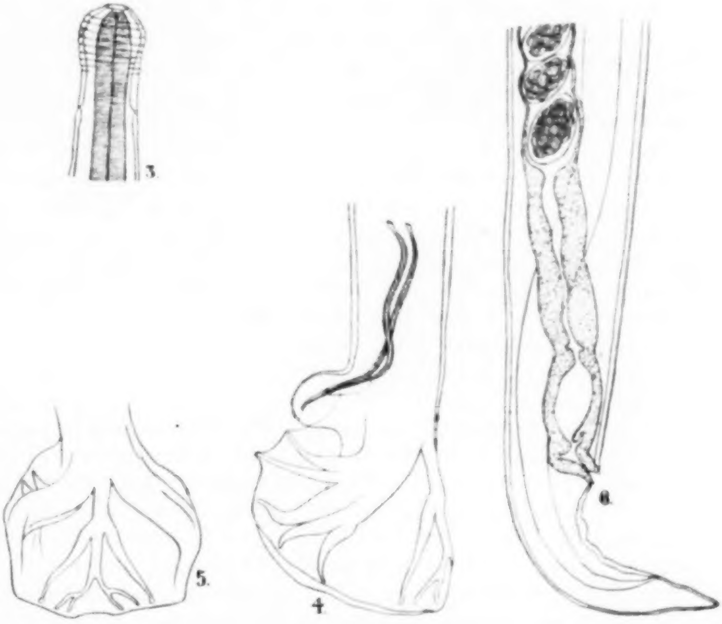
Location.—Intestine.

Locality.—Wonderboom, near Pretoria.

Type-species in Onderstepoort Helminthological Collection, No. 2233.

Heligmonella spira, n. gen. n. sp.

Delicate worms of a bright red colour and coiled in a spiral. The cuticle is inflated around the head and bears very conspicuous transverse striations in this region (fig. 2). On the rest of the body the cuticle shows two broad lateral and four narrower submedian longitudinal raised bands which are marked with fine transverse striations. There is a "cervical



Heligmonella spira.

FIG. 3.—Head.
FIG. 4.—Male bursa, lateral view.
FIG. 5.—Male bursa, dorsal view.
FIG. 6.—Hind end of female.

ring" (fig. 3) situated 0·07 mm. from the anterior end in the female and 0·06 mm. in the male, surrounding the body in that region. The head in the female is 0·04 mm. in diameter, and in the male 0·039 mm. The oesophagus is slightly club-shaped; it is 0·46 mm. long in the female and is followed by a uniformly narrow intestine which is pigmented brown. Very minute cervical papillae were seen in the female 0·03 mm. in front of the end of the oesophagus. The male is 5·5 mm. long and 0·1 mm. thick. The bursa is well developed, but the dorsal lobe is not marked off well

from the lateral lobes. The ventral and lateral rays arise from a common trunk. The ventrals are of approximately the same size, divergent, the latero-ventral carries the edge of the bursa into a point projecting beyond its general contour. The postero-lateral diverges from the medio- and externo-lateral rays, which run close together and parallel to near the bursal margin where the externo-lateral diverges sharply ventrad, the medio-lateral running practically straight to near the edge (fig. 4). The externo-dorsal rays are given off from the dorsal stem at about one-third of the distance to the edge of the bursa and reach very near to the margin; the dorsal ray bifurcates another third of the distance further on, forming two fairly strong branches which each again bifurcate (fig. 5). The internal surface of the bursa is slightly roughened. There are two equal, slender spicules, slightly coiled and alate, 0·41 mm. long, and a gubernaculum which is boat-shaped. The genital cone is prominent and 0·075 mm. long.

The female is 6·5 to 8 mm. long and 0·11 mm. thick. The tail (fig. 6) is bent ventrad, is pointed, and 0·043 mm. long. The vulva is not very conspicuous and opens 0·165 mm. in front of the tail end; it leads into a strong, short vagina and an ovijector which together are 0·31 mm. long and are continued by a single uterus which runs forward. The eggs are oval, measuring 63 $\mu \times 39$ μ, segmenting when laid.

Host.—***Thryonomys swindernianus*** (Natal Cane rat).

Location.—Stomach and duodenum.

Locality.—Wonderboom, near Pretoria.

Types in Onderstepoort Helminthological Collection, No. 2174.

This genus belongs to the *Heligmosominae* (***Trichostrongylidae***) and is most closely related to the genus *Viannaia* Travassos, 1914, from which it can, however, be distinguished by the marked longitudinal striations of the cuticle which is not very thick, ventral rays not directed forwards, spicules longer and more slender. It may be characterised as follows:—

Heligmonella.—Heligmosominae: body red, spirally coiled, cuticle with marked longitudinal striations; cephalic cuticle inflated and transversely striated. Male: bursa with ventral rays separate and diverging, postero-lateral diverging from externo- and medio-lateral, externo-dorsal arises from a common dorsal trunk, dorsal bifurcated near its extremity, the branches also bifurcated; spicules slender, gubernaculum distinct. Female: vulva near anus, a single uterus. Parasites in stomach and intestine of rodents.

Type-species.—*H. spira* n. sp.

Polydelphis quadricornis (Wedl, 1862).

In his description of the above species, Baylis (1921) remarks on the fact that Wedl states that this species has a four-branched uterus, and

further on he states that " Many specimens have a short intestinal caecum running forward beside the oesophagus, but this feature is apparently not constant." While examining some specimens of *P. quadricornis* from the Puff adder (*Bitis arietans*) in the Onderstepoort Helminthological Collection, the following interesting facts were noted in connection with the above: Of five females four had six uteri, in one case two of the branches were for some distance fused together, and the fifth female had only five uteri; the latter specimen had two intestinal caeca, the one twice as long as the other, while of four other females and four males six had each one caecum. Although six uterine branches is apparently the normal for this species, it does not seem strange to find fewer since polydelphid uteri are formed evidently by branching of the original didelphid uterus.

The Genus *Spirostrongylus*.

Yorke and Maplestone (1926), in their work on the Nematode Parasites of Vertebrates, created the genus *Spirostrongylus* for a Nematode *S. spirostrongylus* from *Macropus* sp. At the time of publication of this book, a paper by the present writer was in the press and shortly afterwards appeared, in which the name *Spirostrongylus* was given to a Nematode named *S. australis* from *Macropus rufus*. Since the two worms in question are not identical and do not belong to the same genus, and since *Spirostrongylus* Yorke and Maplestone, 1926, has preference, I propose for the second species the name *Rugopharynx* (Syn. *Spirostrongylus* Monnig, 1926, not Yorke and Maplestone, 1926).

Type-species.—*R. australis* Monnig, 1926.

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STUDIES IN THE GROWTH OF GRAPES.

By P. R. v. d. R. Copeman, B.A., B.Sc.

(With four Text-figures.)

During the grape season of 1922 the question of the ripeness of grapes arose in connection with their export, and, from this point of view, it is obvious that such terms as "ripe" and "unripe" are capable of a purely arbitrary application. In order to throw some light upon this question, investigations into the changes which occur during the ripening of grapes were undertaken during the 1923 season. The work was continued during the grape seasons of 1925 and 1926 so that some idea might be obtained with regard to the effect of climatic conditions. In order to study the progressive changes which occurred during the ripening process, the analyses were performed at weekly intervals during each of the three periods of investigation. The results included the usual determinations of sugar, acid, total solids, etc., and have been reported on in previous papers.* The data, so accumulated, may be used to show the theoretical significance of the growth changes, and the present paper deals with this aspect of the problem.

The varieties of grapes employed in this work have all been table grapes, since the problem in the first place was confined to this type. The varieties were White Hanepoot, Red Hanepoot, Gros Maroc, Barbarossa, Waltham Cross, and Flaming Tokai, and were obtained during each season from the Government Wine Farm, Groot Constantia. The work done in 1923 was carried out at the farm and was of a preliminary nature. In the other years the work was performed in the Government Chemical Laboratory, Cape Town, and therefore, owing to the better facilities available, more accurate and reliable. In this work no attempt has been made to study the changes which occurred *after* full maturity had been reached. At this stage the grapes were consigned to the press.

Most of the work previously done on grapes has been mainly concerned with the final crop-yield, and such analyses do not show the progressive

* Copeman, Dept. of Agr. Bull., Div. of Chem. Ser. 31, 1924; Copeman and Frater, Sc. Bull. No. 50, Dept. of Agr., 1926; Copeman, "Some Changes occurring during the Ripening of Grapes" (unpublished manuscript).

changes in composition. The changes in composition have been studied for American varieties by Alwood and his associates;* by Bioletti, Cruess, and Davi,† and by Noyes, King, and Martsolf.‡ The European varieties have been studied by, amongst others, Brunel,§ and by Baragolia and Godet.‖ Lewis ¶ has published a paper on the development of grapes in South Africa, but his work was confined to wine grapes. In no one of these cases, however, has any attempt been made to develop the theoretical conception of the changes.

Owing to the fact that the grape samples were all obtained from the same locality, the results for each season are strictly comparable and the effects of seasonal climatic conditions can be studied. In 1923 no rain fell during the period of investigation, and the days were clear and warm. In 1925 thet otal rainfall during the period under review was only 0·21 inch, and this occurred on two days about a week apart near the beginning of the ripening period. In both these years, therefore, the conditions were apparently favourable for photo-synthesis. In 1926 the total rainfall was 2·10 inches and occurred on seven days during the investigation. There were also a large number of cloudy days. The mean temperature was also higher during 1925 than during 1926. The conditions were, therefore, not so favourable to plant development as during the previous seasons. On this account the period of ripening was prolonged and the attainment of maturity somewhat delayed. On the other hand, in 1926 the analyses were commenced about three weeks earlier than in previous seasons, so that a more complete record of the ripening period was obtained. In this connection a paper ** dealing with "Some Effects of Seasonal Conditions upon the Chemical Composition of American Grape Juices" is of considerable interest. Somewhat marked variations are recorded for different seasons. It is stated that "there is a consistent and fairly high degree of correlation between sugar, acid, and total astringent content." It is, therefore, important that, when comparing the results for different seasons, the grapes should be at the same stage of maturity.

In previous papers the changes in the various constituents, as determined, were presented in the form of curves, and the significance of these has been stressed. It has been pointed out that the analytical data cannot be expected to fall completely on a smooth curve. Apart from the almost

* U.S. Bur. Chem., Bulls. 140 (1911); 145 (1911). U.S. Dept. Agr., Bulls. 335 (1916); 452 (1916).

† Univ. of Cal. Pub. in Agr. Sc., vol. iii, No. 6, 1918.

‡ J.A.O.A.C., vol. vi, No. 2, 1922.

§ Rev. de Vit., vol. xxxvii, p. 15.

‖ Landw. Jahrb., vol. xlvii (1914), p. 249.

¶ Bull. Dept. Agr. 69, 1910.

** Caldwell, J. Agr. Res., vol. xxx, No. 12, 1925, p. 1133.

insuperable difficulties of obtaining absolutely representative samples from a product so widely variable as a fruit, there are factors which are quite as important as the method of sampling. In this connection the work of Bioletti, Cruess, and Davi * is significant. They point out that considerable irregularity occurs from week to week. Factors, such as the age of the vine, the position of the bunch on the vine, and of the berry on the bunch, as well as the aspect of the vineyard, all affect the data, and errors due to these sources would be extremely difficult to eliminate. Even when these factors are taken into account there is still some variation in the sugar content of the juice. The smoothed curves, then, may be regarded as approximations which are fully justified by the difficulties involved.

The main conclusions from the work that has been done are that the most important changes which occur during ripening are those which take place in the sugar and acid content of the juice. The sugar increases and the acid decreases during the period of ripening. The increase in the weight of the berry is mainly due to the increase in sugar content, and obviously a similar conclusion applies to the changes in the soluble-solid content of the juice. The present paper deals with the changes in acid, sugar, and soluble-solid content of the juice and the total solids in the berry.

So far as the acidity is concerned, an attempt † was made to express the change of acid with time by means of a simple logarithmic function of the form $C=ke^{-bt}$. It was found that this gave a very close approximation, at least *during the period of ripening*, but that as the grapes approached maturity the calculated curve became too steep, while the experimental curve began to flatten out. This function, therefore, is capable of only a limited application. This was clearly seen during the present season (1926), when an attempt was made to predict the acidity by means of this expression. The more extended period of the investigation brought out clearly the discrepancy which arose as maturity was reached. On this account the simple logarithmic expression has been abandoned, and a search was made for an expression which would account more completely for the changes which occurred.

Since growth is obviously a dynamic process, it follows that some relationship must exist between the changes in the magnitude of the factors involved, the final magnitude, and the total time of growth. On this basis Blackman ‡ evolved what may be termed "the compound interest law," which may be expressed symbolically as $W_1=W_0e^{rt}$, where W_0 is the initial weight and W_1 the final weight of the plant in time "t." "r" is termed the "efficiency index" of the plant and represents the efficiency

* *Loc. cit.*

† Copeman, Trans. Roy. Soc. S. Afr., vol. xiii, 1926.

‡ Blackman, Ann. Bot., 1919, vol. xxxiii, p. 353.

of the plant as a producer of raw material. The value of " r " is naturally affected by external conditions, but there are variations for different plants, and the index is to a large extent characteristic of different species and varieties. This type of equation has been developed more fully by Mitscherlich * in connection with the factors which limit the crop-yield. The yield rises if some lacking factor is added. Mitscherlich sums up this point of view: "The increase of a crop produced by unit increment of the lacking factor is proportional to the decrement from the maximum." This may be expressed as

$$\frac{dy}{dx}=k(a-y) \text{ or } \log(a-y)=c-kx \text{ or } y=a(1-e^{-kx}).$$

Thus, as the factor x increases, the yield of y increases to the maximum "a." This equation is of the type of a unimolecular reaction in which the rate of change diminishes from the start of the reaction. Such an equation was found to be unsuitable for expressing the changes which occurred during the formation of sugar in the grape juice.

Mitscherlich's equation has also been criticised by Briggs,† but the main ground of criticism seems to be the fact that the changes can be equally well expressed by different mathematical expressions such as $y=a+bx+cx^2$ and $y=A_1\frac{x}{x+c_1}$. Briggs points out that Mitscherlich has been inclined to strain the flexibility of his formula by attributing values to the constants which are not in the best accordance with the experimental data. On the other hand formulæ, such as suggested by Briggs, do not indicate the significance of the constants employed.

In practice it has been found that in many cases the growth begins slowly, but goes on at an increasing rate until the products of growth have so accumulated that the rate of growth slows down. These changes are characteristic of an autocatalytic reaction, and it has been shown that, in many cases, the curves of plant growth exhibit this general reverse curve of an autocatalytic reaction. Following the lead of Robertson,‡ a large number of workers have developed this type of equation, namely,

$$\log\frac{x}{a-x}=K(t-t_1).$$

For example, Gregory § has shown that the changes in lengths and areas of the leaves of *Cucumis sativus* may be expressed very clearly by means of

* Mitscherlich, Landw. Jahrb., vol. xxxviii, 1909, p. 537.

† Briggs, Ann. Bot., 1925, vol. xxxix, p. 475.

‡ Robertson, Archiv. fur Entw. der Organ., vol. xxv, 1908, p. 581.

§ Gregory, Ann. Bot., 1921, vol. xxxv, p. 93.

this formula. Prescott * has employed this equation to express the flowering curve for Egyptian cotton. This author points out that an analysis of the curves obtained should indicate the influence of disturbing factors upon the yield of the plant. In a paper by Gaines and Nevens † the use of what may be termed the Robertson equation was fully worked out in the case of the changes occurring during the growth of the sunflower and maize.

This expression has been found to be very suitable for the curve expressing the changes in the sugar content of grape juice and, with a slight modification, the changes in the soluble-solid content of the juice and in the total solids of the berry. If the constants have the value attached to them by Robertson they should be of value in supplementing the data of crop-yield, and emphasising the differences between different varieties. Finally, it was found that an expression closely resembling Mitscherlich's and very similar to the simple logarithmic function was applicable to the changes in acidity. In both these types of equation the constants possess a definite significance which it would be idle to ignore. The present paper deals with the application of these expressions to the changes which occur during the ripening of grapes, and for the sake of convenience the discussion will be divided into four main sections, namely :

(*a*) Acidity of the Juice.
(*b*) Sugar Content of the Juice.
(*c*) Soluble Solids in the Juice.
(*d*) Total Solids in the Berry.

The respective equations will be fully discussed in their order.

(*a*) Acidity of the Juice.

During the period of ripening the acidity decreases, but during the 1926 season the analytical data obtained brought to light a fact which had not appeared in the previous seasons. On account of the early commencement of the work, it was shown that there are at least two well-defined stages in the development of the grape. During the first stage, which might be termed the *initial growing period*, the amount of acid showed an increase. In previous seasons the work was commenced when this stage had already been passed. This point, however, has been mentioned by other workers such as Bioletti, Cruess, and Davi.‡ In the second stage the acidity showed a continuous decrease whose rate became less as maturity was reached.

* Prescott, Ann. Bot., 1922, vol. xxxvi, p. 121.
† Gaines and Nevens, J. Agr. Res., vol. xxxi, 1925, p. 973.
‡ *Loc. cit.*

Lewis * has shown that the period of maximum acidity agrees with the beginning of the *ripening period*. It is clear, then, that two processes are involved in the full growth cycle—first a period of production of acid, and second a period of decrease of acid. Unfortunately the data collected have not been sufficient to elucidate the type of growth change corresponding to the first period. The present work only takes account of the *ripening period*.

The most suitable expression to represent the changes in acidity during the *ripening period* was found to be given by

$$\log \frac{a}{x-a} = k(t-t_1) \quad . \quad . \quad . \quad . \quad . \quad (1)$$

In this expression " a " represents the final value of the acidity, " t_1 " is the time in days from the commencement of observation or from the commencement of decrease of acidity. This is the period during which the acidity reaches the value " $2a$," and " k " represents the velocity constant of the change. From the laws governing chemical equilibria it would be expected that k would be subject to variations according to the conditions. On this account external factors such as temperature, light, and rainfall may be expected to influence the value of " k." Seasonal variations should, therefore, be evident in the results.

Expression (1) may be written in the form

$$x = a(1 + e^{-k\overline{t-t_1}}) \quad . \quad . \quad . \quad . \quad . \quad (2)$$

and this may be compared with the expression in a previous paper,† namely, $x = ke^{-bt}$ (the value of k in this equation differs from that in equation (2)).

It will be seen that the first expression only differs from the original form by the addition of another factor. This factor, however, indicates that there is a definite limit to the decrease in acid and shows that the acid can never absolutely disappear from the grape.

From equation (1)

$$\frac{dx}{dt} = -k(x-a).$$

During the *ripening period*, then, the rate of decrease in acidity is proportional to the excess of acidity over the minimum value. As the acidity decreases the rate of change becomes less, until, at maturity, the change is very small, and practically negligible.

The acidity has been expressed as grammes of tartaric acid per 100 c.c. juice, and the values obtained from the experimental data for the constants for the three seasons are given in Table I. In the table, " t_1 " has been

* *Loc. cit.* † Copeman, Trans. Roy. Soc. S. Afr., vol. xiii, 1926, p. 283.

reckoned in days from the time of commencement of the investigation in each season, and the expressions have been calculated for logarithms to the base 10.

TABLE I.—*Acidity* $\log \frac{a}{x-a} = k(t-t_1)$.

Variety.	Year.	a.	k.	t_1.
White Hanepoot	1923	0·42	0·0234	22·5
	1925	0·40	0·0238	25·0
	1926	0·45	0·0217	36·5
Red Hanepoot	1923	0·36	0·0267	26·0
	1925	0·44	0·0275	28·5
	1926	0·34	0·0193	48·0
Gros Maroc	1925	0·54	0·0243	31·5
	1926	0·64	0·0185	36·0
Barbarossa	1923	0·45	0·0318	21·0
	1925	0·43	0·0288	29·0
	1926	0·56	0·0243	27·5
Waltham Cross	1925	0·48	0·0257	18·3
	1926	0·54	0·0202	30·0
Flaming Tokai	1923	0·48	0·0309	26·5
	1925	0·40	0·0292	33·5
	1926	0·59	0·0242	29·0

When these expressions are plotted in the form of curves it is seen that the agreement between the calculated and experimental figures is very close. For the sake of clarity and convenience the curves have been given only in the case of the results for the 1926 season. (See fig. 1.)

On account of the variation in the time of commencing the investigation in each of the three seasons, the values of "t_1" are only comparable for the different varieties in any one season. Thus, in 1923, the value of "t_1" in days, *i.e.* the interval between the commencement of the work and the half period of the acidity, varies in the following way: 22·5, 26·0, 26·5, 26·5 days for White Hanepoot, Red Hanepoot, Barbarossa, and Flaming Tokai respectively. In 1925 the same interval was 25·0, 28·5, 31·5, 29·0, 18·3, and 33·5 days for White Hanepoot, Red Hanepoot, Gros Maroc, Barbarossa, Waltham Cross, and Flaming Tokai respectively. This shows clearly that Waltham Cross is an early ripening variety, while Flaming Tokai and Gros Maroc are late ripening varieties. The remaining varieties occupy an intermediate position. On examining the curves for 1926 it is seen that there is an initial period where the acid is increasing until a maximum value is reached. The actual ripening period commences when the acidity begins to decrease. On the curves this stage has been marked

A_1 . . . A_6 at the point where the two growth curves cut one another. This clearly shows that Waltham Cross ripens earlier than the other varieties, while the remaining varieties commence to ripen in the following order: White and Red Hanepoots, Barbarossa, Gros Maroc, and finally Flaming Tokai. The length of time, from the point A, taken to arrive at

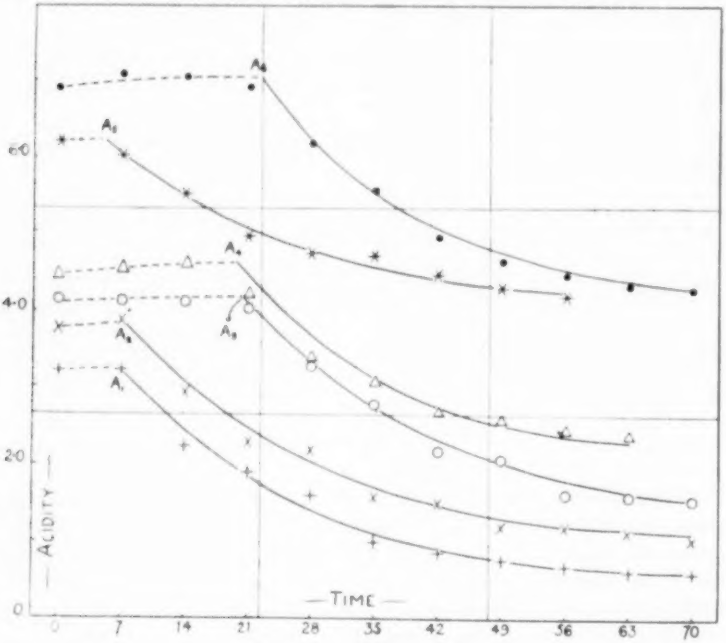


FIG. 1.—Acidity of Juice.

+ White Hanepoot.	
× Red Hanepoot.	Curve = Acid + 0·5.
○ Gros Maroc.	Curve = Acid + 0·5.
△ Barbarossa.	Curve = Acid + 1·5.
✱ Waltham Cross.	Curve = Acid + 3·5.
● Flaming Tokai.	Curve = Acid + 3·5.

the half-value period, varies as follows: 36·5, 48·0, 36·0, 27·5, 30·0, 29·0. In practice the stage A will not be so sharply defined and the curve will show a more gradual change, while the rate of decrease becomes more important than the slowly decreasing rate of production.

In the equation the value of " *a* " represents the minimum value of the acidity during the season, and, on comparing the values given in Table I, it is seen that the value varies slightly according to the variety of grape. For

example, the mean value for the acidity at maturity is 0·42, 0·38, 0·60, 0·48, 0·50, 0·50 for White Hanepoot, Red Hanepoot, Gros Maroc, Barbarossa, Waltham Cross, and Flaming Tokai respectively.

Thus varieties like the Hanepoots, which have a mild sweet flavour, are characterised by a low value of "*a*," while those like Gros Maroc, with a tart flavour, have a high value of "*a*." On the other hand, the value does not seem to be affected to any great extent by seasonal conditions. In an unfavourable season the value is slightly higher than in a favourable season, indicating a slightly more acid product at maturity. The fact that a limiting value is obtained indicates that the change in acidity is subject to some factor whose influence decreases during the process of ripening.

When the values of "*k*" are examined, the variations are much more significant. In favourable seasons the velocity constant of the change is greater than in unfavourable seasons. This result would be expected from the laws governing the dynamics of chemical change. In 1926 the value of "*k*" is less than in the remaining two seasons. It thus appears that seasonal conditions have a direct effect upon the rate of change of the acid. On the other hand, there appears to be only a slight effect upon the actual magnitude of the acidity at maturity. It may, therefore, be concluded that unfavourable seasons cause a retardation of growth and delay in the attainment of maturity. In favourable seasons the reverse is the case. At the same time there seems to be but little effect upon the final composition of the juice at maturity. In this connection the paper * upon "The Effects of Seasonal Conditions upon the Composition of Grape Juices" is of interest. The author draws the conclusion that the variation in composition of the juice is narrower under constant cultural conditions in one locality than in samples grown over a wide area under different cultural conditions. If the grapes are compared at the same stage of maturity it appears that the variations in acidity are even less than hitherto suspected. If comparisons are made at arbitrarily chosen periods in different seasons the differences will naturally be large.

It would seem that those varieties with a longer ripening period are associated with a low acidity at maturity, *e.g.* the Hanepoots. On the other hand, varieties such as Flaming Tokai have a short ripening period, but a higher acidity at maturity. A low rate of ripening is associated with a low value for the acidity at maturity. From this point of view the values of the velocity constant should serve a useful purpose in crop studies.

The conclusion drawn at the end of the first paper † still remains valid, namely, that at maturity the change in acidity becomes negligible and there is little further decrease in acidity. The conclusions which have been

* Caldwell, *loc. cit.*

† Copeman, Trans. Roy. Soc. S. Afr., 1926, vol. xiii, p. 297.

drawn in the present paper are applicable to the ripening period of the berry, but, if the conditions are altered and further *normal* growth is inhibited, then an entirely new set of factors has to be considered and the exponential law, as here derived, will no longer be applicable.

(*b*) Sugar Content of the Juice.

On examining the curves obtained for the changes in the sugar content of the juice, it was readily seen (particularly in the case of the results for 1926) that any modification of the expression developed for the changes in acidity was not applicable to the sugar curve. It was evident from the curves that there was an initial lag in the rate of production of sugar. An expression, such as Mitscherlich's, presupposes a high initial rate of production, and a curve of this type would give far too short a growing period. The type of curve was the general reverse curve characteristic of growth in plants and animals. Robertson * has shown that such a curve can be represented by the equation of an autocatalytic reaction, and in their paper † Gains and Nevens have applied this equation to the study of the growth of sunflower and maize crops. This form of equation has been found to express very closely the changes which occur in the sugar content of grape juice. If the constants have the significance attached to them by Robertson they should be extremely useful in the study of crops.

If the amount of material at the commencement of such a reaction is represented by "a" and the amount transformed in time "t" be x, the amount of original material left is $a-x$.

The velocity of reaction is catalysed by a product proportional to x, and is also proportional to the amount of material $a-x$. The velocity of reaction is therefore

$$\frac{dx}{dt}=kx(a-x) \quad . \quad . \quad . \quad . \quad . \quad (1)$$

where "k" is the velocity constant of the reaction. It is clear that the rate of the reaction will increase with time until $x=a-x=\frac{a}{2}$, after which time the velocity will decrease.

By integration

$$\log\frac{x}{a-x}=\mathrm{K}(t-t_1) \quad . \quad . \quad . \quad . \quad . \quad (2)$$

in which $\mathrm{K}=ka$ and $t=t_1$ when $x=\frac{a}{2}$. "t_1" is the time in which "a" is half transformed and may be regarded as the half-value period.

* Robertson, *loc. cit.* † Gaines and Nevens, *loc. cit.*

In the latter form the equation is applicable to observed data. In the general form of the curve there are two asymptotes, one at 0 and the other at "a." In the present work the time, reckoned in days, has been taken from the commencement of the work as origin. The approximate constants obtained from the curve have been corrected by the method of least squares. In regard to the significance to be attached to the constants, "a" is the final resultant of the growth processes and, according to Robertson, is subject to a considerable degree to modification by external conditions. On the other hand, "k" is regarded as a specific constant, representing inherent qualities of growth. Since $K = ka$, the value of "k" may be estimated from the values obtained by observation. Robertson infers that the value of "k" is a constant which is independent of environment. Reed and Holland * maintain that the rate of growth in the Helianthus is controlled by some internal factor or factors which are of such importance that the external factors are overbalanced, provided that the latter do not approach too closely the maximum or minimum values. This view cannot be regarded as entirely correct. In the first place their investigation was confined to the study of one variety of Helianthus, and in the second place their statement regarding the external factors is equivalent to specifying given conditions. In this latter case a constant value of "k" would be expected for a given plant. From the point of view of chemical dynamics variations of k with external conditions (*e.g.* temperature) would be expected. Prescott in his paper † on the "Flowering Curve of Egyptian Cotton" gives figures which show that "k" is subject to variation according to external conditions.

In practice attention is generally paid to the final growth attained by the crop, and in general this is identical with "a." From the relationship $K = ka$ it is apparent that the constant "k" varies in an inverse ratio to the crop yield. A high value of "K" means a short growing period, and consequently a short growing period tends to be associated with a low crop yield. "k" is a constant representing the inherent growth *velocity*. Conversely $\frac{\text{"}a\text{"}}{K}$ varies directly with the crop yield and is somewhat better adapted for purposes of comparison. It is also a constant representing the inherent growth *capacity*. Its value as an index of growth capacity depends upon the association between the length of the growing period and the final extent of growth. It represents the inherent capacity for crop yield and should serve as a means of comparison between different varieties of plants under comparable conditions. Since the growth-rate of a plant varies with the age of the plant as well as with the seasonal conditions, it would not be

* Reed and Holland, Proc. Nat. Acad. Sci., 5, 1919, p. 135.

† Prescott, Ann. Bot., 1922, vol. xxxvi, p. 121.

expected that these data would be absolutely constant. Thus in crop studies the variations in these quantities may possess a practical significance.

The results have been expressed as grammes of invert sugar per 100 c.c. juice, and the constants obtained from the experimental data are given in Table II, having been calculated for logarithms to the base 10; and time reckoned in days from the commencement of the work.

TABLE II.—*Sugar.* $\log \frac{x}{a-x} = K(t-t_1)$.

Variety.	Year.	a.	K.	t_1.
White Hanepoot	1925	20·25	0·0392	8·0
	1926	21·82	0·0383	26·0
Red Hanepoot . .	1923	20·40	0·0383	0·5
	1925	19·85	0·0385	5·5
	1926	21·05	0·0373	25·5
Gros Maroc . .	1925	18·45	0·0435	11·5
	1926	16·10	0·0427	31·5
Barbarossa . .	1923	17·10	0·0430	4·0
	1925	17·85	0·0447	11·0
	1926	18·10	0·0427	31·0
Waltham Cross . .	1925	20·00	0·0358	8·0
	1926	19·50	0·0347	21·0
Flaming Tokai . .	1923	19·60	0·0462	5·0
	1925	18·70	0·0466	11·0
	1926	17·00	0·0435	31·0

When these expressions are plotted in the form of curves it is seen that there is close agreement between the calculated and experimental figures. For the sake of clarity and convenience only the curves for 1926 have been given. (See fig. 2.)

On account of the short period over which the experiments were carried out in 1923 and 1925, the form of equation adopted has been assumed to be the same as for the 1926 results. The constants were calculated on this assumption. The initial slow increase of sugar and the final decrease in production of sugar can be clearly seen in the curves for 1926.

As is the case of the acidity the values for "t_1," the period when half the final amount of sugar has been formed, are only comparable amongst themselves for a given season. The data for 1923 have been introduced into the tables but, owing to the difficulties under which the work was performed, the results may be regarded as approximations. In comparing the values of the "half period" for 1925, the following values are obtained :—

8·0, 5·5, 11·5, 11·0, 8·0, 11·0 for White Hanepoot, Red Hanepoot, Gros Maroc, Barbarossa, Waltham Cross, and Flaming Tokai respectively. These figures show that the six varieties may be divided into early and late ripening varieties. The Hanepoots and Waltham Cross reach the "half period" at an earlier date than the remaining three varieties. In 1926

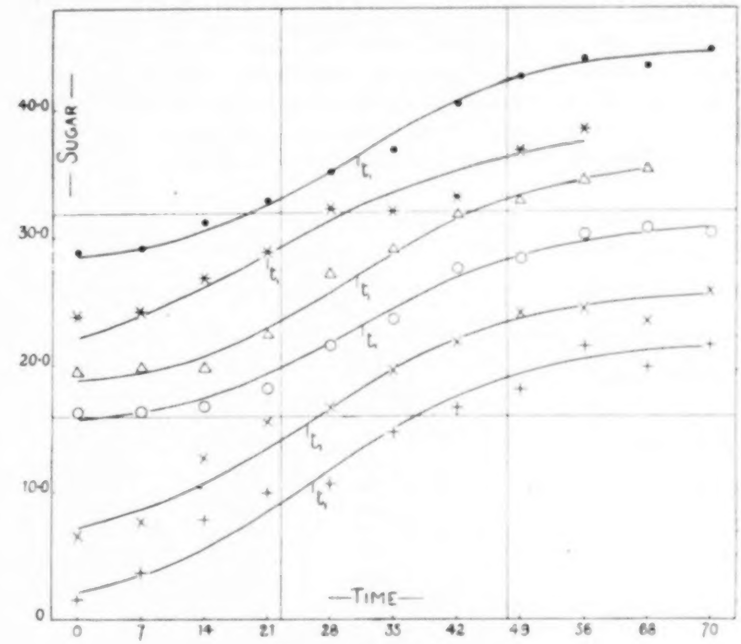


Fig. 2.—Sugar in Juice.

+ White Hanepoot.	
× Red Hanepoot.	Curve = Sugar + 5·0.
○ Gros Maroc.	Curve = Sugar + 15·0.
△ Barbarossa.	Curve = Sugar + 18·0
✳ Waltham Cross.	Curve = Sugar + 19·0.
● Flaming Tokai.	Curve = Sugar + 28·0.

the values were: 26·0, 25·5, 31·5, 31·0, 21·0, and 31·0 for the varieties in the same order. The same distinction can again be made, but in this case the early ripening characteristics of Waltham Cross are more clearly evident.

In the equation "*a*" represents the final yield of sugar, and, in comparing the values given in Table II, it will be seen that the Hanepoots are characterised by the high value of "*a*," indicating that this variety of grape has a high sugar yield. On the other hand Gros Maroc has a low value of "*a*."

It will, therefore, be seen that grapes with a high sugar content have a low acid content and vice versa. On comparing the values of " a " for the three seasons for a given variety, it will be seen that they vary slightly, indicating a seasonal variation. In general the longer growing period is associated with a larger ultimate sugar yield. It would appear that, the more rapidly the products of the growth change appear, the sooner is the rate of change slowed down. The fact that " a " is the limiting value of the sugar content in the juice indicates that there is some factor which tends to prevent a limitless production of sugar in the same way that the acidity is limited.

However, as a more general comparison between the different varieties, the values of the growth *velocity* constant may be compared. This value, calculated from the expression $K = ka$, is given in Table III.

TABLE III.

Variety.	Year.	k.	$\frac{a}{K} \times 10^{-2}$.
White Hanepoot	1925	0·00193	5·17
	1926	0·00180	5·69
Red Hanepoot	1923	0·00188	5·33
	1925	0·00196	5·09
	1926	0·00177	5·64
Gros Maroc	1925	0·00236	4·24
	1926	0·00265	3·77
Barbarossa	1923	0·00252	4·00
	1925	0·00250	4·00
	1926	0·00236	4·24
Waltham Cross	1925	0·00179	5·59
	1926	0·00180	5·60
Flaming Tokai	1923	0·00236	4·24
	1925	0·00249	4·02
	1926	0·00256	3·91

On comparing the values for each variety, it is clearly seen that those with a long growing period are characterised by a high final yield of sugar. It will also be seen that the velocity constant " k " varies slightly according to the season. It would thus appear that this value is subject to some seasonal variation. Under unfavourable circumstances the value of " k " is low, so that the attainment of maturity is retarded. How far this factor is affected by environment, apart from climatic conditions, is a problem which requires further investigation.

If the value of " k " is known, the rate at which the growth products

are being formed can readily be determined. The rate of growth is initially slow, but gradually increases and finally becomes again slow, so that, at maturity, the rate of growth becomes practically zero. These changes are clearly shown in fig. 3, where the rates are plotted against the time (for convenience the corresponding dates are used) in the case of Red Hanepoots. The total time during which the full cycle of changes takes place is known

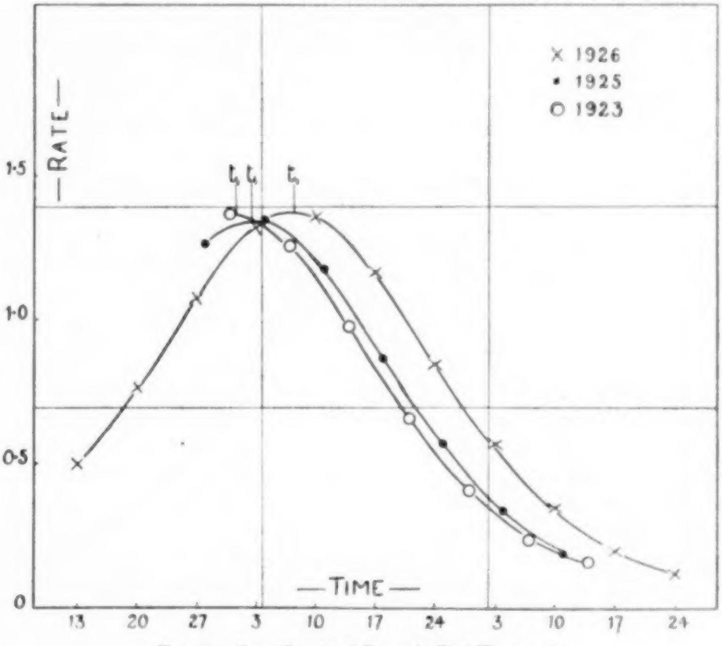


FIG. 3.—Growth-rate of Sugar in Red Hanepoot.

as " the grand period of growth." In the figures the point of maximum rate of growth coincides with the " half period " of the growth. It is clearly seen that the date of maximum growth is later in 1926 than in 1923 and 1925, indicating the retarding power of an unfavourable season. The same results are obtained with the other varieties.

When the growth-rate curves for all the varieties are compared for a given season, the characteristic differences between them can be clearly seen. In fig. 4 the curves for 1926 are given (this season was chosen since a more complete record was obtained). The six varieties can be grouped into two classes which are distinctive. The Hanepoots and Waltham Cross

are early ripening varieties compared with Gros Maroc, Barbarossa, and Flaming Tokai, and the maximum growth-rate is attained in the former at an earlier stage than in the latter varieties. The former also exhibit a longer "grand period of growth" and, in accordance with the theoretical deductions, are associated with a higher ultimate sugar yield. The Hane-

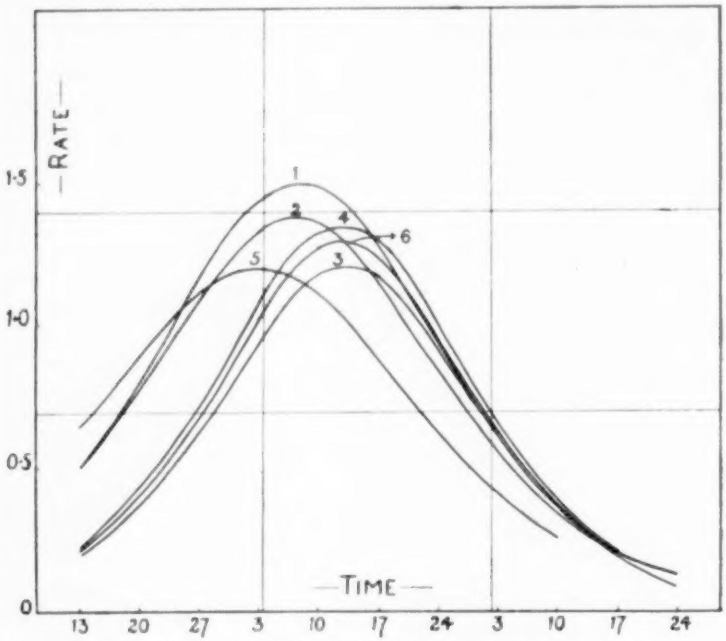


FIG. 4.—Growth-rates of Sugar for 1926.

1. White Hanepoot. 2. Red Hanepoot. 3. Gros Maroc. 4. Barbarossa. 5. Waltham Cross. 6. Flaming Tokai.

poots are characterised by a higher growth-rate at the "half period" than any of the remaining varieties.

As a final comparison between the different varieties, the value of $\frac{\text{“}a\text{”}}{K}$ may be considered. This factor, representing the final growth capacity of the berry, is an inherent characteristic and varies directly with the crop yield. It should, therefore, form a direct means of comparison between the different varieties under comparable conditions. The values obtained are given in Table III. In the first place it is seen that rapid growth is

associated with a low crop yield. For example, the Hanepoots have a low value of "k" but exhibit a high yield of sugar. On the other hand, a variety such as Flaming Tokai ripens rapidly, but the yield of sugar is lower. In practice, of course, the value of such characteristics depends upon the requirements of the grower, since the flavour of the grapes is dependent upon such factors as the relative proportions of acid and sugar.

When the "grand period of growth," as shown by fig. 3, is examined (for 1926, say) it is found that the formation of sugar is spread over a period of approximately fourteen weeks. From this it follows that by about the end of December the amount of sugar formed is practically negligible. The berry obviously commences growth at a very much earlier period, and it is justifiable to assume that the sugar only commences to be formed in appreciable amounts after the berry has reached a definite stage of development. It is clear, then, that the growth of the berry may be divided into two distinct cycles, which may be conveniently termed the *growing* and the *ripening periods*. During the *growing* period acid is being formed, while the sugar is formed at a later stage. Evidence in favour of such a view of the growth of the berry will be given in a later portion of this paper.

(*c*) Soluble Solids in the Juice.

On attempting to apply the Robertson equation to the changes which occur in the soluble solids in the juice, it was found that the agreement between the calculated and observed values was extremely poor. However, by means of a slight modification, Robertson's form of the equation could be utilised to give a very close agreement with the experimental values. This change was effected by deducting an initial value from the reading so that the following modified expression was found suitable :—

$$\log \frac{x-c}{(a-c)-(x-c)} = \mathrm{K}(t-t_1) \qquad (1)$$

where c is the initial value to be subtracted. Equation (1) simplifies to

$$\log \frac{x-c}{a-x} = \mathrm{K}(t-t_1) \qquad (2)$$

By differentiation

$$\frac{dx}{dt} = k(x-c)(a-x)$$

where "k" is the specific velocity constant of the change. It follows that the rate of increase of soluble solids is an autocatalytic change which is proportional to (*a*) the amount of material which has been formed in excess

of some minimum value, and (*b*) to the deficiency from the maximum yield. From the equations it can be readily seen that

$$K=k(a-c) \text{ and } t=t_1 \text{ when } x=\frac{a+c}{2}.$$

It is clear that this equation is only applicable to the observational data when x is greater than " c "; in other words, the soluble solids must have a value of " c " before the changes, represented by the above equation, take place. It follows, then, that this cycle of growth does not commence from the initial stages of growth of the berry and that there is an initial-growth cycle which culminates in a final growth yield of " c " soluble solids. When this stage has been reached a second-growth cycle commences, and this cycle ends with a final growth yield of $(a-c)$ soluble solids or, finally, a total production of " a " grammes of soluble solids for the two cycles. This is in complete agreement with the deductions made from the changes in sugar and acid content of the juice. Apparently, during the initial cycle of growth, the main products are the proteins and acids. The value " c " then represents the amount of soluble solids at the stage when the sugars commence to be formed. On account of the times at which the investigations were commenced, no data are available for an examination of the changes which occur during this initial period of growth. It is natural to assume a zero value for the soluble solids at the origin, and possibly some expression such as $\log \frac{c}{c-x}=kt$ would meet the case.

The data which have been used in the present paper have been obtained from the density of the juice. By means of tables this was converted into grammes of soluble solids per 100 c.c. of juice. This was experimentally shown during the 1926 season to give values which agreed fully within the limits of error with the determined value.

The values for the constants calculated from the experimental data for the three seasons are given in Table IV (p. 285), in which the time has been reckoned in days from the commencement of the investigation in each season. The expressions have been reduced to logarithms to base 10.

When the calculated values are plotted, their agreement with the observed values is seen to be very close. On account of the time at which the work was commenced in 1923 and 1925 the initial lag in the curve is not evident, but the results have been calculated on the assumption that the type of change found in 1926 is equally true for the remaining seasons. The slow increase in the soluble solids from the initial value c can clearly be seen.

From Table IV it is seen that the value of " c " is very nearly 4·0 per cent. If now this value be compared with the values of the acid and

TABLE IV.—*Soluble Solids in Juice.* $\log \frac{x-c}{a-x} = K(t-t_1)$.

Variety.	Year.	c.	a.	K.	t_1.
White Hanepoot	1925	3·86	22·46	0·0380	8·0
	1926	3·85	24·50	0·0379	28·5
Red Hanepoot	1923	3·87	23·00	0·0360	2·0
	1925	3·90	22·10	0·0360	7·5
	1926	3·84	23·55	0·0362	26·5
Gros Maroc	1925	4·28	21·10	0·0413	15·0
	1926	3·95	18·35	0·0410	31·5
Barbarossa	1923	3·20	20·48	0·0410	9·0
	1925	3·80	20·20	0·0416	13·5
	1926	3·50	20·10	0·0414	31·0
Waltham Cross	1925	3·55	21·00	0·0352	9·0
	1926	3·70	21·20	0·0329	20·0
Flaming Tokai	1923	3·50	22·60	0·0410	9·0
	1925	4·62	22·75	0·0456	15·5
	1926	4·04	20·00	0·0396	33·5

protein content of the juice, it will be seen that the soluble solids at this stage consist almost entirely of acid and protein. This is shown in Table V where the figures are given for 1925, when determinations of the protein nitrogen of the juice were made. From the figures it would seem that, during the first cycle of growth, the soluble material produced consists mainly of these two substances. It is only at a later stage that sugar begins to be formed in appreciable quantities.

TABLE V.

	White Hanepoot.	Red Hanepoot.	Gros Maroc.	Barbarossa.	Waltham Cross.	Flaming Tokai.
Acid	3·24	3·40	3·72	3·37	3·29	4·20
Protein	0·22	0·16	0·19	0·14	0·20	0·22
Sum	3·46	3·56	3·91	3·51	3·49	4·44
"C" (Table IV)	3·86	3·87	4·28	3·80	3·55	4·62

The differences between the third and fourth rows are small and may be partly accounted for by the presence of mineral salts in the juice. It is clear that the amount of sugar in the juice at this stage must be practically negligible.

In the expression used "a" has the same significance as in the case of

the sugar. It represents the maximum growth attainable by the berry in the form of soluble solids under the conditions of experiment. At the same time it must be remembered that it represents, in this case, the growth yield as the final resultant of two growth cycles. The crop yield of the second cycle is equal to $(a-c)$.

Since $K=k(a-c)$, the value of "k," the velocity constant of the second change, may be readily obtained from the experimental data. The values of "K," "k," and "a" will be subject to the conditions of environment in the same way as in the case of the sugar constants. In the present case the growth capacity constant, as calculated from the expression $\frac{\text{“}a-c\text{”}}{K}$, represents the constant for the second cycle of growth, and is an index of the crop yield of the second cycle. It depends upon the association between the duration of this cycle and the final extent of growth during this particular period.

In the expression $t=t_1$ when

$$x=\frac{a+c}{2},\ i.e.\ x=\frac{a-c}{2}+c.$$

From this it follows that t_1 is the "half period" of the change from a concentration "c" to the final concentration "a." In the present work the value of "t_1" is only comparable in a given season owing to the variations in the time of commencing the work during the three seasons. The value of "t_1" is expressed in days from the commencement of the work, and on comparison of the values it will be seen that the same division could be made, as in the case of the sugars, into early and late ripening varieties. On comparing the values for the soluble solids with the values of "t_1" for the sugars, it will be seen that the "half period" in the former case is, in general, slightly later than in the latter case. This indicates a slight lag in the rate of change of the soluble solids behind the change in sugar content of the juice. If the "grand period of growth" be taken into account, it will be seen that the time of growth for the second cycle is approximately the same as the "grand period of growth" for the change of sugar content. A retardation of the "half period," according to season, is evident. These facts indicate that there is an extremely close relationship between the content of sugar and total soluble solids in the juice. On comparing the growth-rate curves for the sugar and the soluble solids in the juice it will be seen that, during the initial period of increasing growth-rate, the soluble solids show a lower growth-rate than the sugar. This is due to the fact that the acid is decreasing rapidly during this period. When the rate of decrease of the acid becomes negligible the rate of production of sugar and soluble solids becomes practically identical.

From Table IV it can be seen that the final growth yield as given by "a" varies in the same way as in the case of the sugars and differs from the value for the sugar by approximately 2 per cent. At maturity, then, about 90 per cent. of the soluble solids consists of sugar. The value of "a" varies with the variety of grape as would be expected, and there are also slight seasonal variations. It is also seen that a high crop yield is associated with a long growing period. If the values of "k" as given in Table VI are compared, it will be seen that the velocity constant of the change has a value which is characteristic of the variety. It is not, however, absolutely constant, but is subject to seasonal variations whose effects are not, however, extremely large.

TABLE VI.

Variety.	Year.	$k = \frac{K}{a-c}$.	$\frac{a-c}{K} \times 10^{-2}$
White Hanepoot	1925	0·00204	4·90
	1926	0·00188	5·32
Red Hanepoot	1923	0·00188	5·32
	1925	0·00198	5·05
	1926	0·00184	5·44
Gros Maroc	1925	0·00246	4·07
	1926	0·00285	3·51
Barbarossa	1923	0·00237	4·22
	1925	0·00254	3·94
	1926	0·00249	4·02
Waltham Cross	1925	0·00202	4·95
	1926	0·00190	5·26
Flaming Tokai	1923	0·00215	4·65
	1925	0·00251	3·98
	1926	0·00250	4·00

The value of "k" is very nearly the same as the value for the change in sugar, and it seems clear that the major proportion of the changes which take place in the juice is due to the changes in the sugar content. These latter are so great as to impress their character upon the whole course of change during the ripening period.

As a more suitable means of comparison, the values for the growth-capacity constant of the second cycle of changes in the soluble solids may be compared. The values given in Table VI show clearly that a high value is associated with a long growing period. The value is practically the same as the value for the sugars, and the order in which the varieties may be placed is also the same. It would appear, then, that this constant offers a

convenient means of comparison between different varieties under different conditions.

On comparing the values of the constant of the reaction "K" for the changes in sugar, acid, and soluble solids, it was found that the constant for the soluble solids was practically the arithmetic mean of the constants for the sugar and acid. In other words, the change in the soluble solids is almost entirely due to the changes which take place in the sugar and acid content.

It is found that

$$K_3(s+a)=K_1s+k_2a,$$

where K_1, k_2, K_3 are constants for the sugar, acid, and soluble solids and s and a are the final growth yields of the sugar and acid respectively.

The values for K_3, calculated and observed, are given in Table VII.

TABLE VII.

Variety.	Year.	K_3 *obs.*	$K_3=\frac{K_1s+k_2a}{s+a}$.
White Hanepoot	1925	0·0380	0·0380
	1926	0·0379	0·0375
Red Hanepoot	1923	0·0360	0·0376
	1925	0·0360	0·0374
	1926	0·0362	0·0364
Gros Maroc	1925	0·0413	0·0415
	1926	0·0410	0·0403
Barbarossa	1923	0·0410	0·0405
	1925	0·0416	0·0430
	1926	0·0414	0·0410
Waltham Cross	1925	0·0352	0·0344
	1926	0·0329	0·0332
Flaming Tokai	1923	0·0410	0·0445
	1925	0·0456	0·0450
	1926	0·0396	0·0407

It may, therefore, be concluded that the changes which take place in the juice during ripening are almost entirely those due to the sugar and acid, and that the changes in the other constituents are of little importance. As a matter of fact this conclusion agrees with the data which have been obtained and is in agreement with the conclusions of other workers. For example, Bioletti, Cruess, and Davi * find that the cream of tartar showed

* Univ. of Calif. Pubs. in Agr. Sc., vol. iii, No. 6, 1918.

very little increase during ripening; in most cases the final amount of cream of tartar was less than 0·80 per cent. (grammes per 100 c.c.). Frater * found that the average ash content of 44 varieties of ripe wine grapes was only 0·23 per cent. Lewis † states that the ash content increases on an average by about 50 per cent. during ripening. Since at maturity the ash content of the juice was only about 0·30 per cent., the whole increase could have little effect upon the quantitative yield of the berry. In a previous paper ‡ it was shown that during 1925 the change in the total ash of the berry was on an average from 0·25 per cent. to 0·50 per cent. At the same time the protein content of the juice was found to vary irregularly, any increase being very small and the total protein content of the juice was close to 0·20 per cent.

It would be expected, then, that the conclusions as shown by Table VII should be applicable. It can, therefore, be seen what an important bearing the content of sugar and acid has upon the development of the grape.

(*d*) Total Solids in the Berry.

On attempting to apply the Robertson equation in its unmodified form to the changes which take place in the total solid content of the berry, it was found that the values for the constants were impossible, *e.g.* 35 per cent. approximately of total solids were required as the final growth yield. The calculated velocity constant was too great and the calculated values did not show any agreement with the observed values. By deduction of an initial value from the readings, an expression was obtained which gave figures in agreement with the observed values.

Therefore the change in total solids could be expressed by

$$\log \frac{x-c}{a-x} = K(t-t_1)$$

and the rate of growth by

$$\frac{dx}{dt} = k(x-c)(a-x),$$

where $K = k(a-c)$ and $t=t_1$ when $x=\frac{a+c}{2}$.

The constants in these expressions have the same general significance as in the case of the soluble solids in the juice "a" represents the final yield of dry matter in the berry, where it is the resultant of two growth cycles. The first growth cycle is completed by the production of c grammes

* Dept. of Agr. Bull., Div. of Chem. Ser. No. 33, 1924.

† Bull. Dept. of Agr. No. 69, 1910.

‡ Copeman and Frater, Dept. Agr. Sci., Bull. No. 50, 1926.

of dry matter, and the second growth cycle is characterised by the further formation of "$a-c$" grammes of material. During the second growth cycle, then, the rate of production of material is proportional to the increase of dry matter over the initial value "c," and also to the deficiency from the maximum of the complete cycle.

The total solids are expressed in terms of dry weight per 100 grms. of berry.

The constants, calculated from the observed data, are given in Table VIII. The results for 1925 and 1926 only have been given since adequate facilities for carrying out such a determination were only available during those seasons. The time has been reckoned in days from the commencement of the work, and logarithms to the base 10 were used.

TABLE VIII.—*Total Solids in the Berry.* $\log \frac{x-c}{a-x} = \mathrm{K}(t-t_1)$.

Variety.	Year.	c.	a.	K.	t_1.
White Hanepoot	1925	5·70	22·70	0·0326	6·5
	1926	6·05	24·80	0·0325	32·0
Red Hanepoot	1925	6·30	22·35	0·0318	7·0
	1926	6·25	24·05	0·0322	28·0
Gros Maroc	1925	6·90	21·20	0·0330	16·5
	1926	6·72	20·43	0·0365	30·0
Barbarossa	1925	5·85	20·35	0·0321	12·0
	1926	6·43	22·55	0·0345	33·0
Waltham Cross	1925	7·00	22·40	0·0303	12·0
	1926	6·85	21·60	0·0301	22·0
Flaming Tokai	1925	7·88	22·82	0·0342	13·5
	1926	7·92	22·10	0·0353	35·0

When these expressions are plotted the close agreement between the observed and calculated results is seen.

From Table VIII it will be seen that the first growth cycle leads to the formation of about 6 to 8 per cent. of dry matter before the second cycle commences. The value of this varies according to the variety of grape. On account of the difficulty of determining the exact amount of juice in the berry, it is not possible to show an exact quantitative relationship between the changes in dry matter in the berry and the changes in the soluble solids in the juice. This is also true on account of the changes which take place during the growth of the seeds. For practical purposes the seeds have little significance and determinations of the changes in the seeds were only carried out in 1925 and then allowed to lapse.

From the above table it will be seen, on comparing the value of "t_1" with the value obtained for the soluble solids, that the "half period" for the total solid transformation is practically identical with that for the soluble solids. This indicates that the "grand period of growth" for the second cycle is practically the same as for the soluble solids. In other words, the changes which occur in dry matter take place during the same period as the changes in soluble matter. This indicates that the two changes are probably due to the same cause, namely, the change in sugar and acid content of the juice. The actual growth rates are not in agreement for the reasons given above, but the ultimate effect of the changes in soluble solids can be clearly seen by comparing the values for "the grand period of growth."

As an index for comparison the values for "k," the velocity constant, and "$\frac{a-c}{K}$", the growth capacity of the second cycle, may be taken. The values obtained from experiment are given in Table IX.

TABLE IX.

Variety.	Year.	k.	$\frac{a-c}{K} \times 10^{-3}$.
White Hanepoot	1925	0·00192	5·21
	1926	0·00178	5·62
Red Hanepoot	1925	0·00190	5·26
	1926	0·00181	5·53
Gros Maroc	1925	0·00231	4·33
	1926	0·00266	3·76
Barbarossa	1925	0·00222	4·51
	1926	0·00214	4·67
Waltham Cross	1925	0·00197	5·08
	1926	0·00204	4·90
Flaming Tokai	1925	0·00230	4·35
	1926	0·00248	4·03

From this it will be seen that a high crop yield is associated with a long growing period. On comparing the values of "k" for the total solids with the value for the soluble solids, it will be seen that the former value is very nearly the same as the latter. Therefore it would seem the changes in the total solids are mainly due to the changes which occur in the soluble solids, which in turn are mainly due to the changes in the sugar and acid content of the juice. During the ripening period the changes in sugar content are relatively of such a magnitude that they are the cause of practically the whole of the second cycle of growth in the berry.

As would be expected, the growth capacity constant for the total solids has a higher value than for the soluble solids, but the relatively small difference indicates the very important part which the sugar plays in the growth of the grapes. The value of the growth capacity constant as a means of comparison between the different varieties can be clearly seen by reference to Table IX. It would appear that this constant has equal significance for the several constituents to which this particular type of growth equation applies. It forms a direct means of comparison between the different varieties.

Summary.

The changes which take place during the ripening of grapes have been studied for the three seasons 1923, 1925, and 1926. The varieties of grapes employed in this investigation have been: White Hanepoot, Red Hanepoot, Gros Maroc, Barbarossa, Waltham Cross, and Flaming Tokai. The data which have been studied in this paper are: the acidity, the sugar and soluble solids in the juice, and the total solids in the berry.

Initially the acid in the juice shows an increase, but when the grapes begin to ripen, the acidity decreases. During this period of decrease the changes in the acid content of the juice may be expressed by means of the equation

$$\log \frac{a}{x-a} = k(t-t_1).$$

As full maturity is reached the decrease in acid becomes negligible and the acid approaches the minimum value "a." This value and the constant "k" vary slightly according to the season. These two values are also dependent upon the variety of grape.

The changes in the sugar content of the juice may be expressed by means of the equation

$$\log \frac{x}{a-x} = \mathrm{K}(t-t_1).$$

The rate of production of sugar increases initially to a maximum value and then, as maturity is reached, decreases, and finally becomes negligible. The value "a" represents the ultimate yield of sugar. The growth velocity constant and the growth capacity are represented by the quantities $\frac{\text{"K"}}{a}$ and $\frac{\text{"}a\text{"}}{\mathrm{K}}$ respectively. These quantities give a useful means of comparison between the different varieties, and for different seasons, since they are affected by seasonal conditions.

The changes in the sugar and acid content of the juice clearly indicate

that the growth of the berry may be divided into two periods, which may be termed the growing period and the ripening period.

The changes in the soluble solid content of the juice may be expressed by means of the equation

$$\log \frac{x-c}{a-x} = \mathrm{K}(t-t_1).$$

This expression is only applicable when x is greater than c, and this indicates that there is an initial cycle of growth which results in the production of c grammes of soluble solids per 100 c.c. of juice. This cycle would correspond to the "growing period," and it would seem that during this cycle the main products formed are protein and acid, and that the production of sugar is practically negligible.

The ultimate yield of soluble solids, the growth velocity constant, and the growth capacity of this second growth cycle are respectively "$a-c$," $\frac{\text{"K"}}{a-c}$ and $\frac{\text{"}a-c\text{"}}{\mathrm{K}}$. These quantities are also dependent upon the variety of grape and upon seasonal conditions.

It has been found that the changes in soluble solids are almost entirely due to the changes which take place in the sugar and acid content of the juice.

The changes in the total solids in the berry may be expressed by means of the equation

$$\log \frac{x-c}{a-x} = \mathrm{K}(t-t_1).$$

This expression resembles the expression for the soluble solids in the juice. It also indicates that the growth of the berry may be divided into two cycles. The first growth cycle results in the production of "c" grammes of solids, and the second cycle yields "$a-c$" grammes of solids. The total production of the two growth cycles is thus "a" grammes.

The growth velocity constant and the growth capacity of the second growth cycle are similarly $\frac{\text{"K"}}{a-c}$ and $\frac{\text{"}a-c\text{"}}{\mathrm{K}}$. They also vary according to the variety of grape, and according to the season, and form a useful means of comparison.

In general it may be stated that a low growth velocity constant is associated with a high ultimate yield, and with a long "grand period of growth."

In conclusion the author would like to thank Dr. B. de C. Marchand for the interest he has taken in the preparation of this paper.

Division of Chemistry, Cape Town.

AN EARLY EMBRYO OF THE BLUE WHALE.

By E. L. Gill, D.Sc.

(With four Text-figures.)

The whale embryo here figured was presented to the South African Museum in October 1925 by Messrs. Irvin and Johnson, having been taken from a Blue Whale (*Balaenoptera sibbaldi*) brought in to their whaling station at Saldanha Bay. So far as I have been able to ascertain from the available records it is much the youngest Blue Whale embryo that has been examined; very possibly the youngest embryo of any whalebone whale. The early stages of the toothed whales are better known; a porpoise embryo at about the same stage of development was figured and described by Guldberg and Nansen,* and an interesting comparison is thus rendered possible. It is hardly surprising that early embryos of the larger whales are not secured. In this case the parent whale was about 60 feet in length; the membranous sac enclosing the embryo was an inch long and the embryo itself a quarter of an inch. To recognise and secure such an object in the course of commercial operations at a factory is an achievement that deserves recognition.

The elliptical sac in which the embryo lay was presumably the amnion. For an amnion it was exceptionally large in relation to the embryo, but there was no torn edge or other trace of an investing membrane apart from it, and it was thin and translucent. The embryo was attached to its inner wall considerably nearer one end than the other. The attachment was so close that the embryo could only be described as tightly bound to the wall; there was no sort of body stalk or umbilical cord. The other foetal membranes and the yolk sac were missing.

The embryo itself, as preserved, measures 6·5 mm. in its greatest length. A peculiar feature which it presents is a strong twist in the middle of the body. The coiled hinder half is closely attached to the amnion, and the head and anterior half of the body, which are free, are rotated through an angle of about 120°, so that they face in almost the opposite direction to the hinder half. It is natural to suppose this twist to be due to an

* Development and Structure of the Whale, Part I. Bergens Museum, 1894.

accident in handling during or after removal from the uterus, but examination of the parts and attachments about the region of the twist reveals no sign of violence, and the condition is apparently an exaggerated case of the

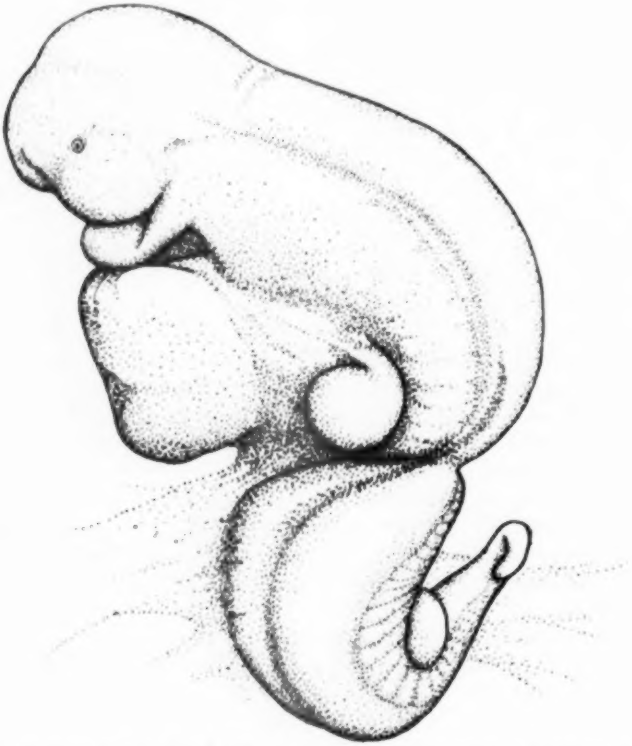


FIG. 1.—Embryo of Blue Whale, *Balaenoptera sibbaldi*. General view of embryo, showing twisted constriction in middle of body. Nineteen times natural size.

dorsal kink and spiral coiling which are sometimes found in early embryos of man and other mammals.

Owing to the twist it is impossible to view the whole embryo at once in any one regular aspect, but a general view is shown in fig. 1. It will be seen that the twist has caused a constriction in the middle of the body. The muscle segments (mesoblastic somites) of the left side are seen as a faintly segmented band running down from the "shoulder" region to disappear in the constriction; while the muscle segments of the right side come into

view behind the constriction and continue down the curved abdominal region into the tail.

The head is seen partly from behind, and its structure will be better understood from the front view given later (fig. 2). The large prominence below the head is the heart. Behind the heart and close to the constriction is the fore limb, at this stage a round bud. Below the constriction the body is much more rapidly curved and the muscle segments more sharply marked. Where the abdominal region merges into the tail there is a conspicuous rounded-conical protuberance which at a first glance might well be taken for the hind limb. On examination, however, it proves to be a median structure. It is the genital papilla, always a prominent feature in whale

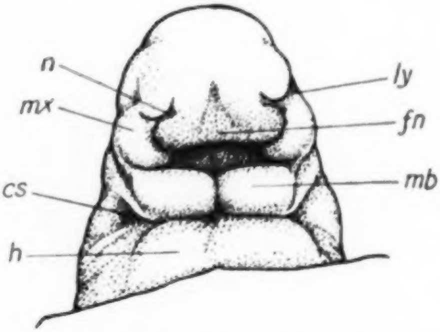


FIG. 2.—Embryo of Blue Whale. Head seen from the front. Eighteen times natural size; *cs*, cervical sinus; *fn*, fronto-nasal process; *h*, heart; *ly*, lachrymal groove; *mb*, mandibular arch; *mx*, maxillary process; *n*, nasal pit.

embryos. From the region where the twist has occurred, bands of thickened tissue containing vessels spread to some distance over the amnion.

The front view of the head, shown in fig. 2, is particularly interesting. The two sides of the mandibular arch (*mb*) have just met in the middle line, but are still hardly completely fused. The upper border of the mouth is formed by the fronto-nasal process (*fn*); the two halves of the upper jaw (maxillary processes, *mx*) are still far apart on the sides of the head. The fronto-nasal process curves up at each side into a shallow pit (*n*), the beginning of the nostril.

The eye is very small compared with that of most vertebrate embryos. A shallow ("lachrymal") groove runs forward from it and curves round to the nasal pit or nostril. The two very large rounded lobes seen in side-view below the eye are the developing maxilla and the outer end of the medial bar of the mandible which forms the lower border of the mouth. The lateral bar of the mandibular arch lies immediately below and behind

these lobes, separated from them by a deep groove except at its distal end, where it is continuous with the medial bar. None of the following arches —the hyoid and the branchials—are visible; they are presumably greatly reduced and sunk in the deep triangular cervical sinus which adjoins the mandibular arch behind. From the point of view of comparative embryology this constitutes the most remarkable feature of the whole embryo (compare fig. 4, C). Almost as remarkable is the straightness of the neck; I do not know of any figured example of an early mammalian embryo which shows the head so little bent forward on the body.

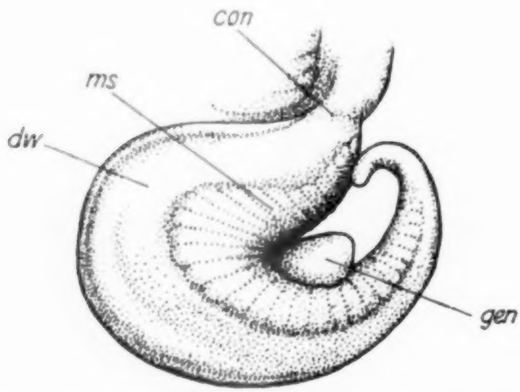


FIG. 3.—Embryo of Blue Whale. Hinder portion of body. Eighteen times natural size; *con*, twisted constriction; *dw*, dorsal body wall; *gen*, genital papilla; *ms*, muscle segments.

The hinder end of the embryo, the part behind the constriction, is shown in direct side-view from the right in fig. 3. The noteworthy features of it are the great transverse width and narrowness of the muscle segments and their position on the inside instead of the outside of the curve, the prominence of the genital papilla, and the absence of a hind limb. In toothed whales at this stage there is a distinct though very small hind limb-bud (fig. 4, A, *hl*), which soon disappears; it lies close to the genital papilla. In this specimen there is no trace of it. Possibly the whalebone whales have lost it altogether, or it may appear a little later.

It is a curious and interesting fact that early embryos of all the higher vertebrates are of practically the same size at corresponding stages of development, irrespective of the size of the parent animals. The Blue Whale is the largest animal in the world, but its embryo conforms to the same rule. It is of about the same size as the corresponding stage, for

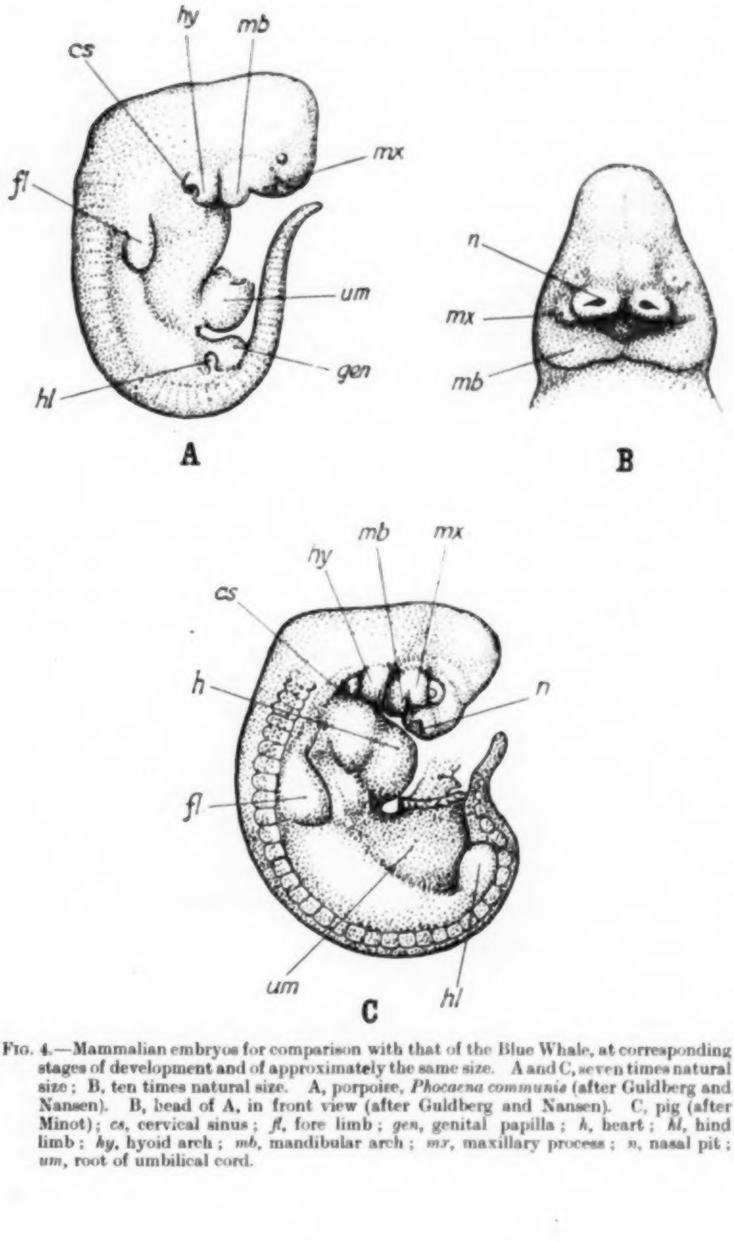


FIG. 4.—Mammalian embryos for comparison with that of the Blue Whale, at corresponding stages of development and of approximately the same size. A and C, seven times natural size; B, ten times natural size. A, porpoise, *Phocaena communis* (after Guldberg and Nansen). B, head of A, in front view (after Guldberg and Nansen). C, pig (after Minot); *cs*, cervical sinus; *fl*, fore limb; *gen*, genital papilla; *h*, heart; *hl*, hind limb; *hy*, hyoid arch; *mb*, mandibular arch; *mx*, maxillary process; *n*, nasal pit; *um*, root of umbilical cord.

example, in the chick, in the rabbit and pig, and in man. Fig. 4 represents embryos at the same stage of development of the common porpoise of the North Atlantic and of the pig. In comparison with all of them the Blue Whale embryo shows a remarkable absence of the bend at the neck; and in comparison with the porpoise it is late in beginning to show any special development of the tail. It agrees with the porpoise in the great proportionate size of the elements of upper and lower jaw and in the reduction of the other branchial arches and grooves. But in the main it is a fairly generalised vertebrate embryo. Fig. 4, B, is a front view of the head of the porpoise embryo represented in fig. 4, A. Compared with fig. 2 it shows considerable differences from the corresponding view of the Blue Whale embryo; in fact the front view of the Blue Whale embryo's head at this stage is more like the same view of the human embryo's head than like that of this toothed cetacean.

Some of the features in which this embryo departs from the usual higher vertebrate pattern are suggestive of the adult whale. The small eye and the absence of a hind limb are obvious cases in point. The large jaw rudiments seem also to be prophetic of the enormous development of the jaws in the adult. Similarly the genital papilla, in its altogether exceptional size, is prophetic of the great development of the genital organs, which is one of the many adaptations to a life in the sea exhibited by the whales. The close segmentation of the muscle (mesoblastic) bands is plainly related to the numerous vertebral segments of the adult, and possibly the reduction or suppression of the branchial arches is a preparation for the extreme shortening of the neck characteristic of all cetaceans.

The embryo is at the same developmental stage and of the same size as the chick of the 4th day, the rabbit of the 11th day, and the human embryo at the end of the 4th week. The duration of pregnancy in the Blue Whale is probably about 12 months. According to Hinton * the foetus is fully formed at 13 weeks; it is then about 18 inches long. The young are born at a length of about 22 feet.

I wish to record my thanks to Prof. M. R. Drennan for valuable criticisms of some of my first interpretations of the structure of this embryo.

* Whales of South Georgia. Colonial Office, 1925.

COLOUR AND CHEMICAL CONSTITUTION.

PART XXII.—DICYCLIC AZOMETHINES AND THEIR CONGENERS.

By JAMES MOIR.

In connection with Part XVII, wherein a method of calculating the bands of monocyclic azomethines and azo dyes was presented, I evolved a theory, supported by much work outside my own, according to which colour comes from the existence of two centres in the molecule defined as hapton and auxochrome.

The following new data on substances possessing *two* auxochromes are of interest in regard to the problem. They are arranged along with those of monocyclic substances possessing the same colour, whereby the search for a probable explanation of the facts is facilitated.

TABLE I.

Group No.	Formula of Substance (all *para*).	Central $\lambda\lambda$.
I.	$O : CHC_6H_4ONa$	330.
	$PhCH : CHC_6H_4ONa$	330.
	$NaOC_6H_4CH : CHC_6H_4ONa$	370 and 330.
II.	$O : NC_6H_4ONa$	400.
	$PhCH : NC_6H_4ONa$	367 and 393.
	$NaOC_6H_4CH : NC_6H_4ONa$	434 and 406.
	$PhN : NC_6H_4ONa$	433 and 395.
	$Me_2NC_6H_4CH : CHC_6H_4ONa$	400.
	$Me_2NC_6H_4N : CHC_6H_4ONa$	433 and 405.
	$(Me_2NC_6H_4CH :)_2$ free base	400.
	$HOC_6H_4CH : CHC_6H_4NHMe_2\bar{A}$	360 and 400.
III.	$O : CHC_6H_4NHMe_2\bar{A}$	359.
	$PhN : CHC_6H_4ONa$	360.*
	$PhCH : CHC_6H_4NHMe_2\bar{A}$	355.
	$HOC_6H_4CH : CHC_6H_4NHMe_2\bar{A}$	400 and 360.
	$NaOC_6H_4CH : CHC_6H_4ONa$	330 and 370.

* Possibly a double band.

IV.	$O : NC_6H_4NHMe_2\bar{A}$	458.
	$Me_2NC_6H_4N : NC_6H_4NHMe_2\bar{A}$	488 and 456.
	$Me_2NC_6H_4N : CHC_6H_4NHMe_2\bar{A}$	496 and 464.
	$HOC_6H_4CH : NC_6H_4NHMe_2\bar{A}$	490 and 460.
	$PhN : CHC_6H_4NHMe_2\bar{A}$	430 and 460.
	$HOC_6H_4N : CHC_6H_4NHMe_2\bar{A}$	435 and 465.
	$Me_2NC_6H_4CH : CHC_6H_4NHMe_2\bar{A}$	430 and 461.
	$NaOC_6H_4N : NC_6H_4ONa$	487 and 455.
	[$PhN : NC_6H_4OH_2Cl$	491 and 461.]
V.	$PhN : NC_6H_4NHMe_2\bar{A}$	507 and 543.
	$Me_2NC_6H_4N : NC_6H_4NHMe_2\bar{A}$	505 and 540.
	$HOC_6H_4N : NC_6H_4NHMe_2\bar{A}$	570, 507, and 540.
Exceptional . .	$PhCH : NC_6H_4NHMe_2\bar{A}$	482 and 514.

The following comments may be useful :—

(*a*) From Group I the cause of the 330 band is the auxochrome ONa along with the double bond.

(*b*) From the first part of Group II we see that the same arrangement gives a band at 400 when CH is replaced by N.

(*c*) From Group III we see that the change of auxochrome from ONa to $NHMe_2\bar{A}$ raises the band from 330 to 360 : similarly arise the high values in Groups IV and V.

(*d*) A special explanation of the stilbene derivatives is called for : their colours are higher than those of hydroxy- and dimethylamino-benzaldehyde, which would not be the case if the central double bond were the sole seat of the action. Apparently the bond next further out (between C_6H_4 and CH) is what co-operates with the auxochrome in these cases.

(*e*) Similarly the bond between C_6H_4 (or Ph) and N must be what co-operates with the auxochrome in the case of those of Group V.

An interesting experimental fact is that tetramethyldiaminoazobenzene, when dissolved in glacial acetic acid, not only shows the strong bands mentioned (Group V, No. 2), but shows also a band in the highest red (λ 685). Substance No. 3 of that group also shows a high band (λ 692), but only with concentrated sulphuric acid. Both of these solutions, even when so strong as to be apparently opaque, are found to pass the extreme red end of the spectrum (λ 740 to λ 800) when examined by sunlight.

As a side-line to this investigation I have roughly examined the twelve other isomers of dihydroxyazomethine (Group II, No. 3), and found that

they differ little in colour from the para-para isomer, although a number of them cannot be represented as quinonoid.

TABLE II.—*Alkaline Dihydroxyazomethines.*

Position of the Hydroxyls.	Position of Band.
2–2′	450
2–3′	510
2–4′	440
2–5′	440
2–6′	420
3–2′	430
3–3′	470
3–4′	410
3–5′	470
3–6′	408
4–2′	420
4–3′	410
[4–4′	434 and 406]

The plain figures are used in numerating the aminophenol ring, and the dashed figures the hydroxybenzylidene ring.

MARRIAGE AND MORTALITY RATES OF THE POPULATION OF THE UNION OF SOUTH AFRICA ACCORDING TO THE CONJUGAL CONDITION OF THE POPULATION.

By C. W. Kops,

University of the Witwatersrand, Johannesburg.

(With two Text-figures.)

A knowledge of the marriage and mortality rates of the population is of great importance when considering any scheme of social insurance. Should a Government wish to introduce some scheme whereby annuities are paid to widows, as is done by many societies, such annuities would most probably cease on remarriage, and it is obviously important to know the rates of remarriage among widows so that proper reserves may be kept and accurate estimates made of the expenditure likely to occur in any particular year. It is, of course, also necessary to know the death rates among widows so as to prevent an unduly large reserve being formed, and the death rates among married men in order to be able to estimate the number of new entries to the group of widows who will require assistance.

This paper is an attempt at calculating such marriage and death rates among bachelors, widowers, spinsters, and widows, and the death rates among married persons. The figures were obtained from the Union Government Census Department. These were, unfortunately, not sufficiently detailed to enable graduation to be done by a mathematical formula. Thus the never-married, married, and widowed populations were obtainable only in quinquennial age groups, and in order to find the populations at each year of age, recourse had to be taken to a graphical method of redistribution. This applies also to the marriages.

Suppose that

$(\mathrm{bL})_x$ = the number of bachelors living aged between x and $x+1$,

$(\mathrm{bm})_x$ = the number of bachelors who marry between the ages x and $x+1$, and that $(\mathrm{mwL})_x$, $(\mathrm{mwm})_x$, and $(\mathrm{sL})_x$, $(\mathrm{sm})_x$, and $(\mathrm{fwL})_x$, $(\mathrm{fwm})_x$, refer similarly to the widowers (male widowed), spinsters, and widows (female widowed) respectively, then

$\frac{(\text{bm})_x}{(\text{bL})_x}$ = the central marriage rate among bachelors aged x to $x+1$,

with similar expressions for the others.

The central death rates have not been found, as the number of deaths was too small for any kind of graduation. I have, however, found what may be called the average death rates over five-yearly periods, by dividing the deaths in any five-year group by the numbers living in that group. This enables one to compare to some extent the mortality among the various classes.

For the numbers marrying and dying I have used the 1921 Census figures, as this year seemed a fairly normal one after the War. For the number living at 1st July 1921 I extrapolated, using the figures of the 1918 and 1921 Censuses.

In Tables I and II are given the graduated values of the numbers living and marrying for bachelors and widowers, and spinsters and widows respectively, and also the ungraduated values for comparison. Table III gives the central marriage rates, and Table IV the quinquennial death rates. Figs. 1 and 2 show the relations between the marriage rates for bachelors and widowers, and spinsters and widows respectively.

It will be seen that the marriage rate among widowers greatly exceeds that among bachelors. The bachelors' rate reaches a maximum value at about age 28, and that of widowers at about the same age. The average age at marriage of the bachelors was about 28·2, and of the widowers about 45·2. The marriage rate for widows similarly exceeds that for spinsters, but the difference is not as great as in the case of bachelors and widowers. The spinsters' rate reaches a maximum value at about age 24, and that of the widows at about age 25. The average age at marriage of the spinsters was about 23·5, and of the widows about 36·6.

It is rather remarkable that the maximum rates of marriage occur at about the same ages for those who have never been married before and the widowed. The only marriage rates I could find for purposes of comparison are those found in the Scottish Bankers' Experience, 1903–23 (T.F.A., vol. x, pt. v), where are given the rates for bachelors and widowers only. The maximum rate ages are again the same for bachelors and widowers, namely 33 years, and again we find that the widowers' rates exceed those for the bachelors. The following table compares the Scottish rates with the South African rates. It must be remembered, however, that the bankers are a very special class, and that marriages among bachelors at least are not allowed until they have reached a certain grade, and this is partly the reason why the maximum rate ages are higher than is the case for a general population.

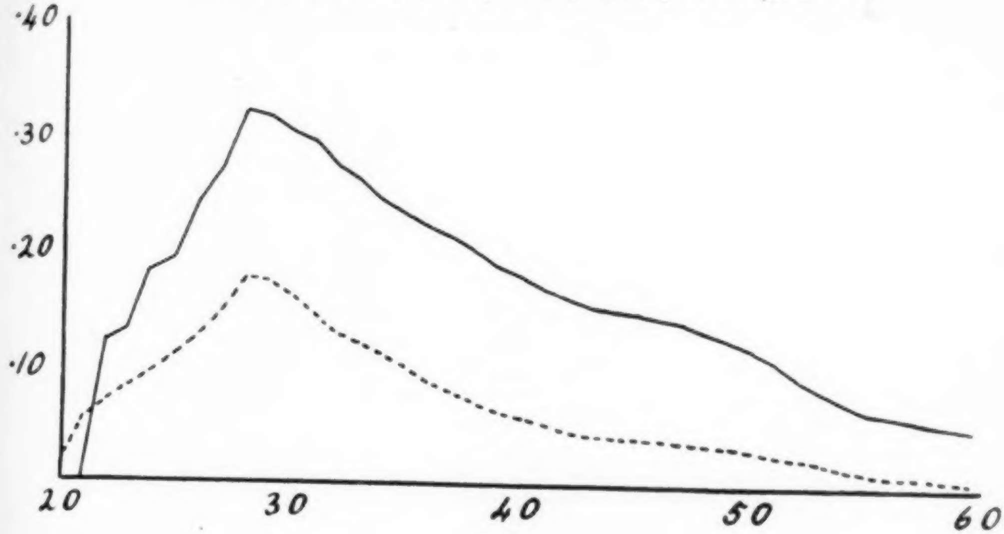


Fig. 1.

———— (m w m r)$_x$ Widowers' marriage rate
- - - - - - (b m r)$_x$ Bachelors' " "

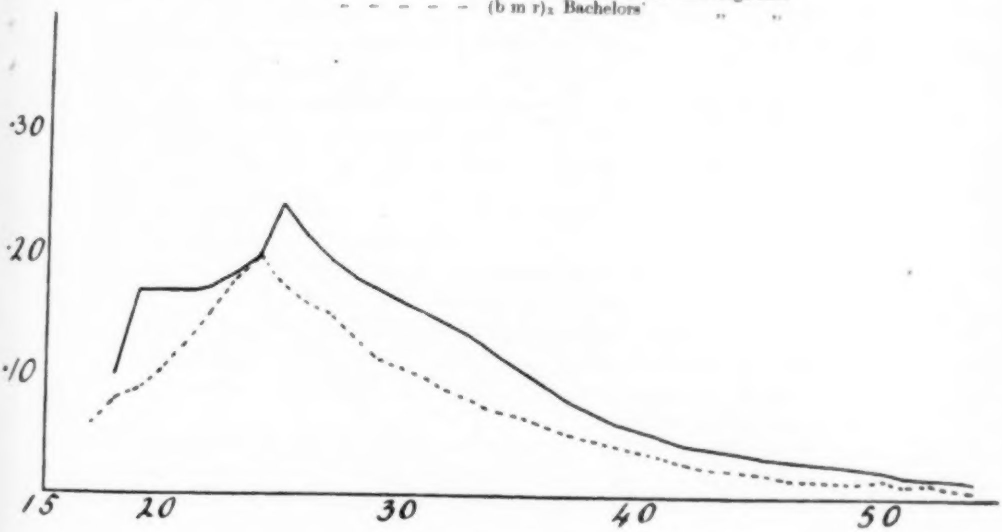


Fig. 2.

———— (f w m r)$_x$ Widows.
- - - - - - (s m r)$_x$ Spinsters.

MARRIAGE RATES (per 10,000).

Age.	South Africa.		Scottish Banks.	
	$(bmr)_x$.	$(mwmr)_x$.	$(bmr)_x$.	$(mwmr)_x$.
20	131	..	15	..
25	1113	..	230	..
30	1635	3070	745	1500
35	1034	2360	725	1470
40	610	1807	495	1350
45	414	1510	330	1140
50	310	1200	230	810
55	143	696	148	540
Max. rate.	1771	3256	850	1500

The South African marriage rates are considerably higher than the Scottish Bankers' rates. This would probably also be the case if we could compare the South African rates with the Scottish general population rates, for, on comparing the crude marriage rates for the two populations, we find that the South African rates are higher than the Scottish rates. I could not obtain any figures more recent than those for 1913.

Crude Marriage Rates.	South Africa.	Scotland.
1911	92	67
1912	96	69
1913	90	71

These are the number of marriages per 10,000 of the population.

A study of the crude marriage rates of various countries seems to show that the younger countries always have a higher marriage rate than the older ones, possibly due to the fact that there are usually more people of marrying age in the younger countries.

It is possible to suggest reasons for the greater marriage rates among the widowed. In the case of the widowers, it must be remembered that these are men who have once been, and probably still are, in a position to

become married; for example, a widower's financial position most probably will still be such as to permit of his supporting a wife, and maybe children, as well as himself. The number of bachelors, however, includes many who may never be in such a position.

Again, a widow is very likely in possession of those qualities which a man looks for in a wife. These may be good looks, good housekeeping capabilities, a thrifty nature, or other virtues; whereas again the number of spinsters includes those who, through lack of attractions, physical or otherwise, are very unlikely ever to get married. Further, there may be children from the first marriage, and their parents will very often feel the need for someone to help bring up and educate these children. This may be one large factor causing widowed persons to marry again.

On examining Table IV we find that the death rate among married men is lower throughout than that of bachelors. This, I may point out, is the experience of many countries as far as I could gather. Married women show a similar advantage over their unmarried sisters, except during the first fifteen or twenty years of married life. This is possibly due to the fact that the mortality due to pregnancy and childbirth is highest at these ages, and that, after those who are physically unfit to stand against these causes of death are "weeded out" (if I may use such a term), the death rates follow a similar trend as in the case of married and unmarried men.

No doubt the married state offers some security against economic hardship for women, and in the case of both women and men it is possible that the more settled existence and need for greater care of oneself owing to the increased responsibilities are advantageous as far as longevity is concerned. Possibly also there are some physiological factors which weigh in favour of married persons, but I am not in a position to explain these.

The figures for widowed persons are not sufficiently reliable for us to draw conclusions from, and this subject must be left until such time when more reliable data are obtainable.

I hope that after the 1926 Census more detailed figures will be available, and that it will then be possible to construct a reliable marriage- and death-rate table. The present figures serve to indicate the trend, but are not suitable for purposes of valuation of annuity and other benefits.

[TABLE

TABLE I.

Age.	$(bL)_x$. Grad.	5-Year Groups. Ungrad.	Diff.	$(bm)_x$. Grad.	5-Year Groups. Ungrad.	Diff.	$(mwL)_x$. Grad.	5-Year Groups. Ungrad.	Diff.	$(mwm)_x$. Grad.	5-Year Groups. Ungrad.	Diff.
20	11,420			150			2			0		
21	10,800			600			4			0		
22	10,120	50,464	+116	740	3186	−36	8	57	− 1	1	10	− 2
23	9,460			808			15			2		
24	8,780			852			27			5		
25	8,000			890			42			8		
26	7,100			920			57			14		
27	6,200	31,038	− 38	936	4457	+ 1	73	363	− 5	20	101	+ 2
28	5,240			928			86			28		
29	4,460			784			100			32		
30	3,730			610			114			35		
31	3,020			448			127			38		
32	2,660	14,167	−117	352	1962	0	141	701	+ 2	39	193	+ 1
33	2,420			298			155			41		
34	2,220			254			166			41		
35	2,070			214			178			42		
36	1,940			178			191			43		
37	1,830	9,062	+158	152	773	+11	205	1020	+ 4	44	220	− 3
38	1,740			130			217			44		
39	1,640			110			233			44		
40	1,540			94			249			45		
41	1,440			78			265			45		
42	1,360	6,849	+ 11	66	351	−13	280	1392	−15	45	224	+ 1
43	1,290			58			289			45		
44	1,230			52			294			45		
45	1,160			48			298			45		
46	1,080			44			303			44		
47	1,020	5,253	−133	40	206	− 6	310	1568	− 4	44	222	− 3
48	960			36			320			43		
49	900			32			333			43		
50	840			26			350			42		
51	780			22			363			40		
52	720	3,606	− 6	18	57	+33	371	1825	0	36	162	+16
53	660			14			373			32		
54	600			10			368			28		
55	560			8			359			25		
56	500			6			351			23		
57	450	2,240	+ 60	5	24	+ 2	345	1729	+22	21	110	− 2
58	410			4			345			20		
59	380			3			351			19		
			+345 −294			+47 −55			+28 −25			+20 −10

Table II.

Age.	$(sL)_x$. Grad.	5-Year Groups. Ungrad.	Diff.	$(sm)_x$. Grad.	5-Year Groups. Ungrad.	Diff.	$(fwL)_x$. Grad.	5-Year Groups. Ungrad.	Diff.	$(fwm)_x$. Grad.	5-Year Groups. Ungrad.	Diff.
17	11,400	11,830	−430	660	685	− 25	5	7	− 2	0	0	0
18	9,900	9,430	+470	770	875	−105	10	12	− 2	1	2	− 1
19	9,400	9,423	− 23	815	793	+ 22	18	16	+ 2	3	2	+ 1
20	8,710			912			30			5		
21	7,900			1000			54			9		
22	6,980	35,015	− 85	1066	5005	+101	88	451	+ 9	15	90	− 6
23	6,120			1084			126			23		
24	5,220			1044			162			32		
25	4,360			770			200			48		
26	3,640			592			240			52		
27	3,080	15,739	+ 81	470	2415	+ 7	280	1423	− 43	55	275	− 4
28	2,580			344			316			57		
29	2,160			246			344			59		
30	1,820			194			370			60		
31	1,580			158			390			60		
32	1,460	7,460	0	130	689	− 9	418	2031	+ 45	59	290	+ 1
33	1,340			108			438			58		
34	1,220			90			460			54		
35	1,120			76			484			51		
36	1,060			64			508			47		
37	1,000	4,989	+ 11	54	259	+ 19	534	2707	− 39	43	221	− 4
38	940			46			560			40		
39	880			38			582			36		
40	820			32			600			34		
41	760			26			620			31		
42	700	3,449	+ 71	20	112	− 4	638	3067	+113	28	136	+ 9
43	640			16			652			27		
44	600			14			670			25		
45	580			12			688			24		
46	560			10			708			22		
47	540	2,763	− 63	8	43	0	726	3705	− 69	21	115	− 9
48	520			7			746			20		
49	500			6			768			19		
50	480			6			800			18		
51	460			5			826			16		
52	440	2,221	− 21	5	24	− 1	848	4362	−144	15	71	+ 3
53	420			4			866			14		
54	400			3			878			12		
55	370			2			890			12		
56	340			1			900			11		
57	310	1,497	+ 13	0	6	− 3	910	4462	+100	10	46	+
58	270			0			924			9		
59	220			0			938			8		
			+646			+149			+269			+18
			−622			−147			−299			−24

TABLE III.—CENTRAL MARRIAGE RATES (per 10,000).

Age. x.	Bachelors. $(bmr)_x$.	Widowers. $(mwmr)_x$.	Spinsters. $(smr)_x$.	Widows. $(fwmr)_x$.
17	..	..	579	0
18	..	..	778	1000
19	..	..	867	1667
20	131	0	1047	1667
21	556	0	1266	1667
22	731	1250	1527	1705
23	854	1333	1771	1825
24	970	1852	2000	1975
25	1113	1905	1766	2400
26	1296	2456	1636	2167
27	1510	2740	1526	1964
28	1771	3256	1333	1804
29	1758	3200	1139	1715
30	1635	3070	1066	1622
31	1483	2992	1000	1538
32	1323	2766	890	1411
33	1231	2645	806	1324
34	1144	2470	738	1174
35	1034	2360	679	1054
36	918	2251	604	925
37	831	2146	540	805
38	747	2028	489	714
39	671	1888	432	619
40	610	1807	390	567
41	542	1698	342	500
42	485	1607	286	439
43	450	1557	250	414
44	423	1531	233	373
45	414	1510	207	349
46	408	1452	179	311
47	392	1419	148	289
48	375	1344	135	268
49	356	1291	120	247
50	310	1200	125	225
51	282	1102	109	194
52	250	970	114	177
53	212	858	95	162
54	167	761	75	137
55	143	696		
56	120	655		
57	111	609		
58	98	580		
59	79	541		

TABLE IV.—DEATH RATES FOR QUINQUENNIAL AGE GROUPS (per 10,000).

Age group.	Bachelors.	Married Men.	Spinsters.	Married Women.	Widowers.	Widows.
20–24	39	34	28	52	74	44
25–29	53	37	37	55	84	51
30–34	100	48	59	66	85	58
35–39	132	66	72	68	98	68
40–44	155	80	88	73	131	82
45–49	180	100	104	83	179	99
50–54	222	138	128	104	219	116
55–59	296	195	172	162	320	149

Note.—The figures for widowers and widows were so scanty that it is not safe to draw any conclusions from the above death rates.

NOTE ON THE ZAAMENKOMST SLAB.

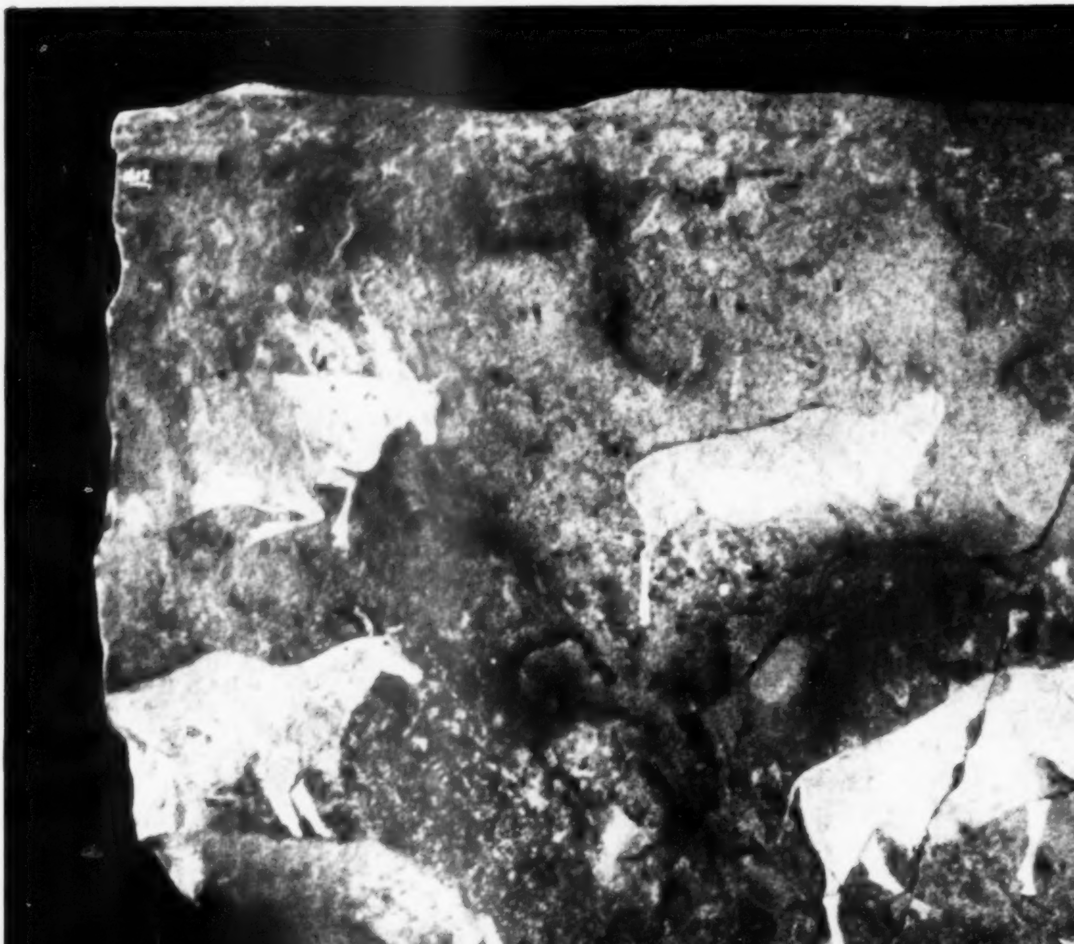
By Dr. Sidney H. Haughton.

The large slab covered with paintings, of which reproductions are given here, has a height of 3 feet and a length of 7 feet 10 inches. It is obviously incomplete, and forms but a part of what must have been a larger mural painting.

The slab, which is in the collection of the South African Museum, was obtained for the Museum in the year 1912 by Mr. G. S. T. Mandy. He discovered it in a cave on the farm Zaamenkomst, which lies about 12 miles from the town of Maclear in Griqualand East. The slab was lying, in two parts, face downwards, in ash which covered the floor of the cave, and must have fallen either forwards from the wall of the cave or downwards from the roof. There is no evidence available to settle this point. From the ash and debris on the floor of the cave no artefacts nor other evidence of occupation have been recovered. No traces of paintings were found on other large slabs which lay in the ash ; but on the walls were remains of other scenes showing an entirely different technique.

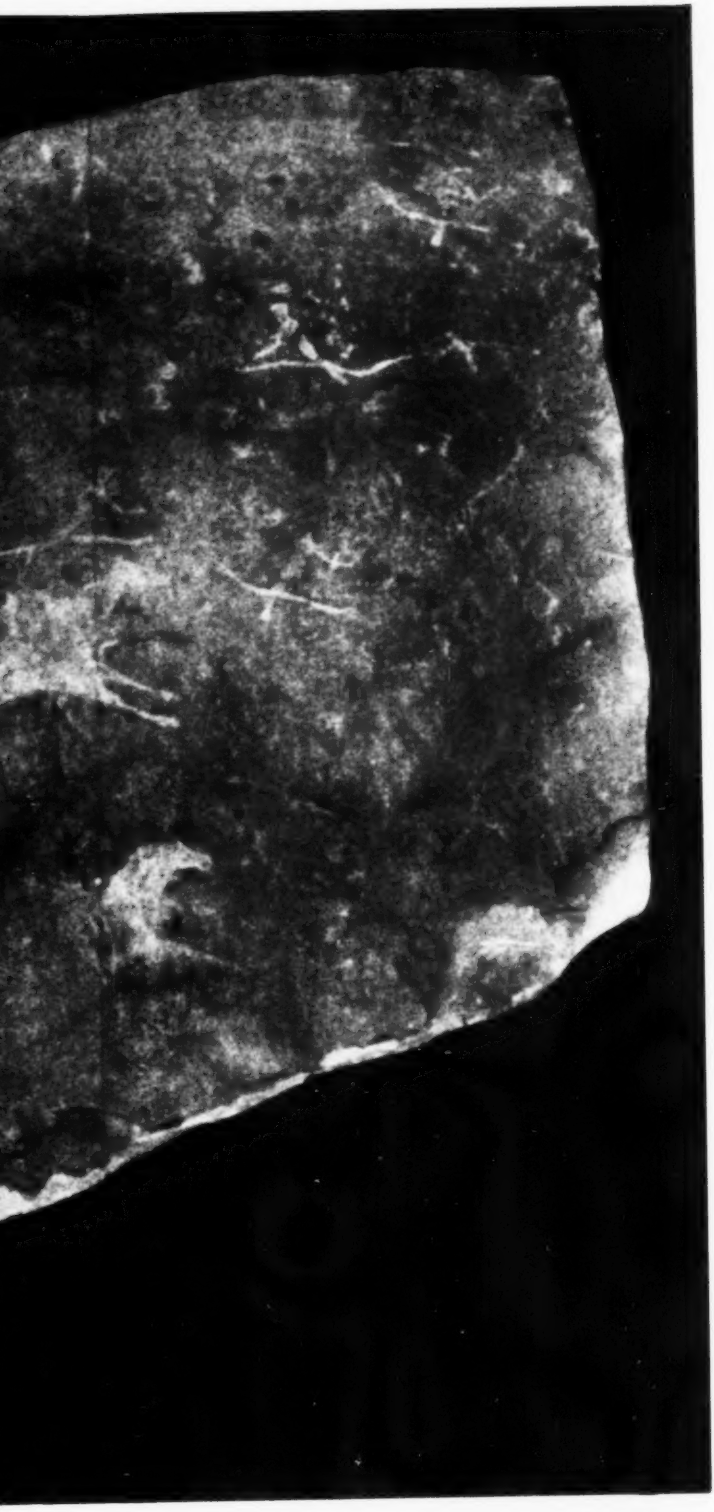
The painting is probably one of the finest of its kind hitherto found in the Cape Province, and is remarkable not only for the colouration but also for the attention paid to details. The nature of the polychrome colouring can be compared with that of the wall-paintings of Altamira.

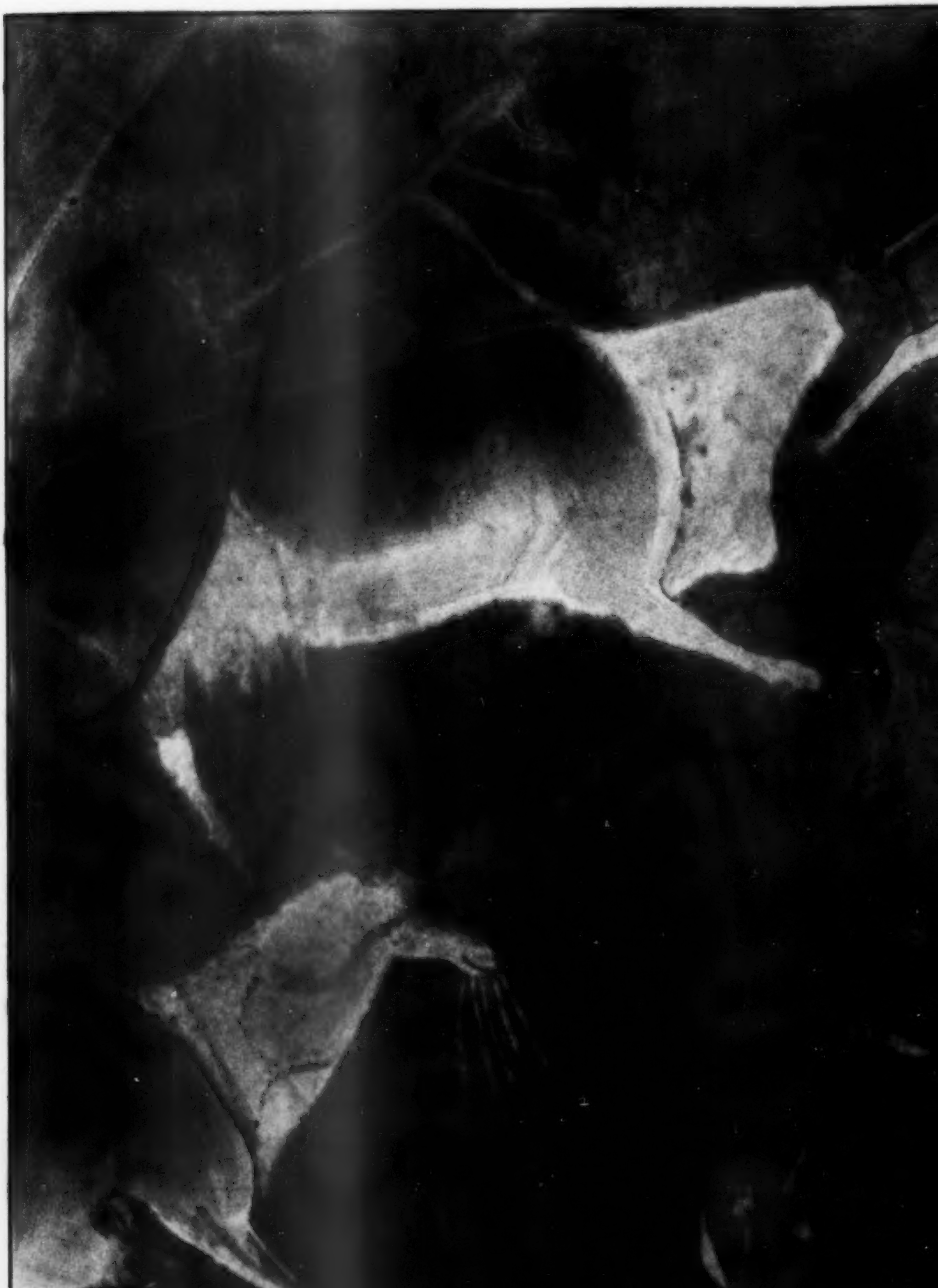
The scene depicted is that of a herd of elands surrounded by hunters armed with bows and arrows and also with battle-axes. The hunters are running rapidly, this impression being conveyed by a conventional drawing of the outstretched legs. The animals are depicted as foaming at the mouth, and, in one instance, approaching death is indicated by the presence of bloody foam. The details of the animal figures are far more realistic than those of the men ; but the presence of head-plumes and battle-axes as part of the equipment of the hunters lends peculiar interest to the scene, for these would seem to indicate that the men were not Bushmen but Bantu. The late Dr. Péringuey considered that the bows and arrows depicted are of the type used by the Barotse and other Zambesi tribes.



1 FOOT

1 METRE.





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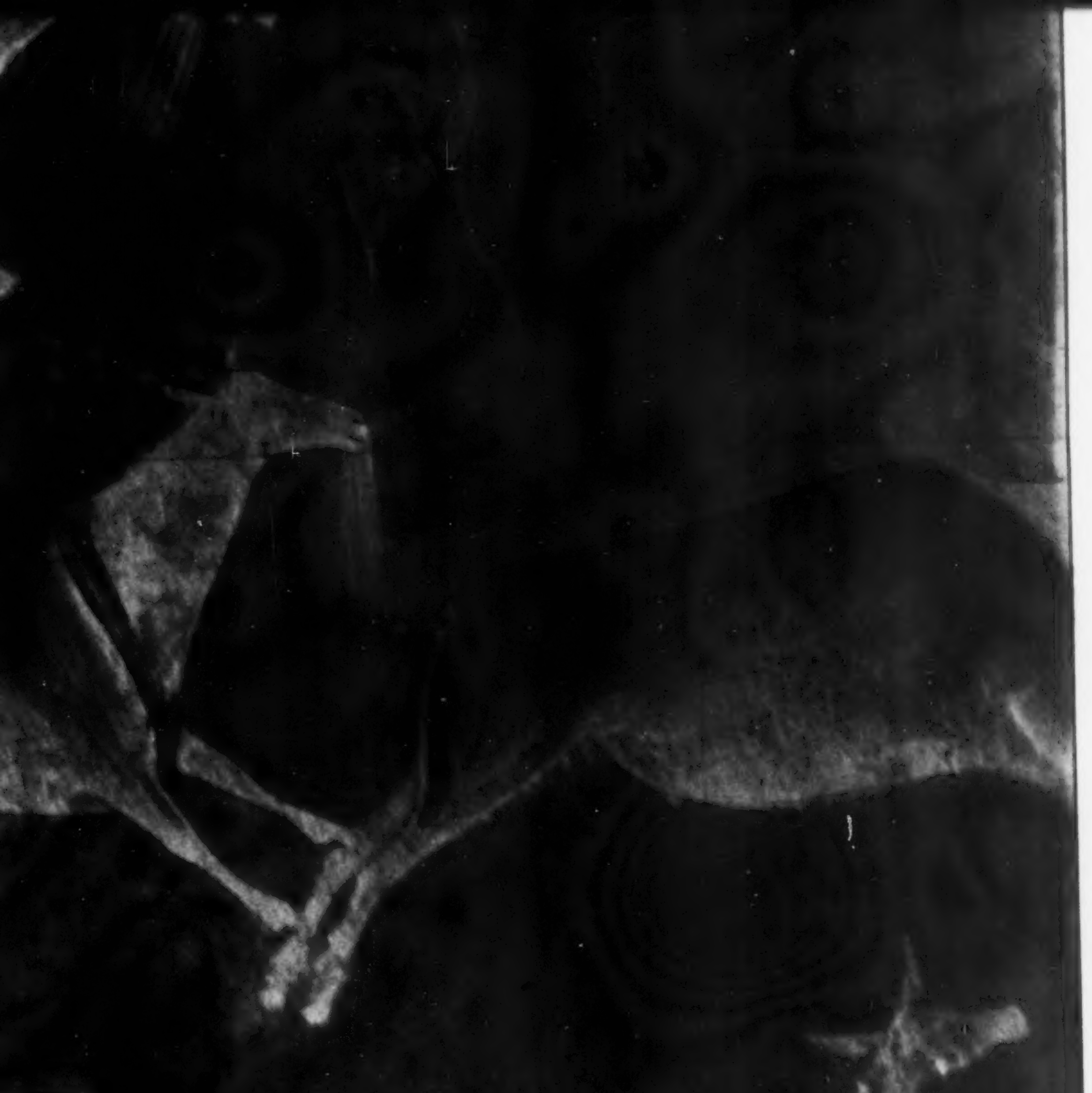

OF ·54 × NATURAL SIZE – ABOUT 5/9.

FAUREA McNAUGHTONII PHILL. ("TERBLANZ"): A NOTE ON ITS ECOLOGY AND DISTRIBUTION.

By John Phillips, B.Sc.(Edin.),
Forest Research Station, Deepwalls, Knysna.

The stately forest tree *Faurea McNaughtonii* Phill. (Proteaceae : sect. Persoonioideae) is of considerable interest on account of its peculiar regional and local distribution. The objects of the present communication are to describe certain ecological features of the tree and to discuss the possible reasons for its interesting distribution.

Distribution.

Kotze and E. P. Phillips (1919, and attached correction 1920) have outlined the regional distribution of the species, showing that it occurs at Gouna (Knysna), Cwebe (Elliotdale), Ntsubani (Lusikisiki), Nenga (Port St. John's), and Ngomi (Northern Natal).

O. B. Miller (1924 : in a letter), until lately Demarcating Officer, Transkeian Forest Conservancy, records the species as occurring in another small forest in the Lusikisiki District.

J. D. Keet (1926 : in a letter), Conservator of Forests, Transvaal and Orange Free State Conservancy, records the occurrence of what he considers to be *F. McNaughtonii*, in the Mariep's Kop Reserve (24° 35′ S. by 30° 55′ E.), "on the slopes (upper) of Magalieskop and also in the patch of detached forest on the plateaux between Magalieskop and Mariep's Kop. . . ."

T. R. Sim (1907 : pp. 297–298) cites McNaughton, Conservator of Forests at the Knysna, 1897–1909, as stating the tree occurred within the Blaauwkrantz Forest, Zitzikamma. Investigation by Conservator Burton and the writer has shown that the trees considered to be *Faurea McNaughtonii* are generally *Pygeum* (the bark of which much resembles that of *Faurea McNaughtonii*), and less often *Scolopia Mundtii*.

Remarks concerning the supposed occurrence of the tree a few miles east of Storms River, Zitzikamma, appear in several Forest Department records, but here again *Scolopia Mundtii* seems to have been confused with it.

The possible reasons for the discontinuous distribution of *F. McNaughtonii* are dealt with in a separate section.

Community Relations.

(1) *At the Knysna.*

Apart from the occurrence of a community of 80–90 saplings and seedlings (the progeny of a single tree wind-blown in 1910), and of a single small tree and several seedlings at Klipkop, Gouna Forest Road, *Faurea* is found within a portion of the Lilyvlei Forest, Gouna, only. In this forest Sim (*loc. cit.*) states that there are some 60 trees only, whereas Marloth (1913: p. 157) cites C. B. McNaughton as estimating the total number at about 30,000.

The writer, on the basis of *absolute frequency* data obtained from a transect 30 acres in area, and with the certain knowledge that the tree does not occur on more than about 1000 acres of the Lilyvlei Forest, finds that the probable number of stems *over* 1 *inch in diameter* at 4½ feet from the ground is not greater than 12,000—about 12·04 trees per acre. When younger plants are taken into account, transect data show that approximately 1·1 plants *from* 15 *feet in height and less than* 1 *inch in diameter* to the *cotyledon-stage seedlings* are found per square yard—that is about 5324 are found to the acre.. The *approximate absolute frequency,* all stages being considered, is 5336 per acre—the total number of individuals on the 1000 acres being within the vicinity of 5,400,000.

Within the Lilyvlei Forest is found the *Faurea McNaughtonii-other* species association. In this community, which is very local even within the best portions of the *Faurea*-clad area, the tree attains full heights ranging from 50 to 80 feet, and girths between 4 and 10 feet at 4½ feet from the ground. The boles are clean, upright, and cylindrical, only occasionally showing vestigial *plank-buttresses*; the crowns are of the inverted-broom shape, with strong lateral arms bearing a wealth of foliage.

The root-systems of the larger trees are best developed 24 to 30 inches below the surface of the soil, that is they are of *medium* depth in the classification of root-systems of the Knysna spp. (J. Phillips, 1926 (1)).

The root-system is heart-shaped with strongly developed laterals. Coppice is produced by felled stumps.

Associated with the *Faurea* as co-dominants are *Podocarpus* spp., *Olea laurifolia, Apodytes dimidiata, Ocotea bullata,* and larger trees of *Pterocelastrus variabilis.* Sub-dominant species are *Plectronia obovata, P. Mundtii, Olea* spp., smaller *Celastraceae, Lachnostylis capensis,* and *Curtisia faginea.* The lower layers are composed of dense *Trichocladus crinitus* (to 15 feet in

height) and *Burchellia capensis* (to 18 feet in height), with which species are mingled saplings of ***Faurea*** and other important trees. The ground vegetation consists chiefly of *Blechnum punctulatum, Gerbera* spp.; *Aspidium capense*, however, is the principal plant on drier sites and *Blechnum capense* holds all the moister ones. Mingled with the ground vegetation proper, are ***Faurea*** and other tree seedlings of various stages.

Adjacent to the small associations above described, are portions of the *Podocarpus Thunbergii-Olea laurifolia-other* spp. association (J. Phillips, 1926 (1)), in which ***Faurea*** is a sub-dominant only. Regeneration of this species is poorly represented in this community.

So far as the 1000-acre portion of Lilyvlei Forest is concerned, the following *percentage frequency* data are of interest in that they show the relative paucity of *Faurea McNaughtonii* :—

Species.	Actual number of trees from 1-inch diameter at 4½ feet from ground, on the 30 acres of the transect.	Percentage frequency.
Olea laurifolia	2599	19·05
Gonioma Kamassi	2243	16·43
Burchellia capensis	1340	9·82
Podocarpus Thunbergii Hook	1287	9·43
Curtisia faginea	738	5·41
Apodytes dimidiata	731	5·35
Olea capensis	690	5·06
Royena lucida	616	4·52
Plectronia obovata	467	3·42
Ocotea bullata	396	2·91
Nuxia floribunda	366	2·68
Faurea McNaughtonii	357	2·61
Elaeodendron croceum	349	2·56
Halleria lucida	306	2·24
Plectronia Mundtii	233	1·70
Platylophus trifoliatus	231	1·69
Ochna arborea	221	1·62
Celastrus acuminatus	146	1·07
Celastrus peduncularis	128	0·94
Podocarpus elongata L'Herit	97	0·71
Pterocelastrus variabilis	92	0·68
Ilex (capensis) mitis	11	0·08
Olinia cymosa	1	0·008
	13,645	99·988

The distribution of the several diameter classes of ***Faurea McNaughtonii***, according to data obtained from the same 30-acre transect, is as follows :—

Diameter classes. Inches.	Actual number of trees in the several classes.	Percentage frequency of the several classes.
1–3	140	39·21
3–5	58	16·24
5–7	31	8·68
7–9	39	10·92
9–11	27	7·56
11–13	14	3·92
13–15	19	5·32
15–17	8	2·24
17–19	4	1·12
19–21	4	1·12
21–23	5	1·40
23–25	1	0·28
25–27	2	0·56
27–29	1	0·28
29–31		
31–33	2	0·56
33–35		
35–37	1	0·28
37–39		
39–41		
41–43	1	0·28
43–45		
45–47		
All classes above 47		
	357	99·97

The distribution of smaller plants of ***Faurea McNaughtonii***, according to the mean data compiled from transects run in various portions of the 1000-acre area of Lilyvlei Forest, is as follows :—

Height classes.	Percentage frequency.
Plants under 12 inches . .	67·59
Plants above 12 but under 36 .	31·29
Plants above 36 but under 72 .	1·12
	100·00

The existence of burnt stumps and of relict trees of ***Faurea*** in the subseral Macchia between the present margin of the Lilyvlei Forest and the Knysna River gorge, indicates that the species less than a century ago had slightly wider limits. The Knysna River gorge and that of the Red Els River may act as barriers to the extension of the limits of the species, but *inefficient migration* and very low *germinative capacity* must be the explanations for the absence of the plant from the other portions of Lilyvlei Forest itself. The sporadic occurrences at Klipkop possibly are to be explained as the result of accidental dispersal of several viable seeds by animal or wind agencies. Thorough examination of the Gouna Forest between the Red Els River and the Klipkop sites has failed to show the presence of any other individuals.

A portion of the 1000-acre area, containing some of the finest of the ***Faurea***, has been marked off as a scientific and scenic reserve—this area (200 acres) will not be disturbed in any manner.

(2) *In the Forests of the Transkeian Conservancy.*

The writer has inquired concerning the sociological characteristics of the species in the forests of the Transkeian Conservancy. From information supplied by O. B. Miller (1924: in a letter) it appears that the plant occurs exceedingly sparsely in the several areas in which it has been recorded. In marked contrast to the conditions prevailing in the 1000-acre portion of the Lilyvlei Forest, Gouna, the trees are very rarely grouped, *single* trees being separated by many hundreds of yards of mixed forest not containing ***Faurea***. Young regeneration is said to be very local and very sparse.

(3) *In the Ngomi Forest; Northern Natal.*

According to information supplied by Forester Tustin (through the kind services of Conservator Boocock), the species occurs as *single* trees separated from one another by dense high forest in which *Syzygium Gerrardi* is the dominant tree. Regeneration is sparse.

(4) *In the Transvaal* (*Mariep's Kop*).

The trees are scattered and not abundant.

Habitat Factors.

The discussion of habitat factors as they influence the species under study is confined to the conditions obtaining within the Knysna region. The prime factors alone can receive treatment.

(1) *Light.*

In the Lilyvlei Forest the regeneration stages experience very low light-intensities (measured per Clement's Stopwatch Photometer).

At noon on a sunny, cloudless day the value at 6 inches above the soil, in the ***Faurea-other*** spp. association with dense 15-feet high layers of ***Trichocladus crinitus***, ranges from $\frac{1}{300}$ to $\frac{1}{400}$; while 20 feet above the ground, among the crowns of the pole stages, the value ranges from $\frac{1}{80}$ to $\frac{1}{120}$. In forest where *Podocarpus Thunbergii* Hook and *Olea laurifolia* are the dominants and ***Faurea*** a sub-dominant—the *Trichocladus* layers being dense—the value at 6 inches is $\frac{1}{350}$ to $\frac{1}{500}$, that at 20 feet, $\frac{1}{100}$ to $\frac{1}{150}$.

The rate of height-increment of the younger stages under such low light-intensities is higher than in the instances of most other native species of the Knysna forests—the first-stage seedlings attaining heights of 5 to 6 inches in one and a half to two years, and the later seedling stages putting on 4 to 8 inches increment in a single year. On sites where the light-intensities are higher, owing to the opening of the canopy by wind or light exploitation, the height-increment is even higher—the first-stage seedlings attaining heights of 8 to 12 inches in one and a half to two years, and the later seedling stages putting on 4 to 15 inches increment in a single year.

The colour of the foliage varies according to the light-intensity.

Two sets of two-year-old seedlings growing within 25 yards of one another on soils of similar physical nature and of identical moisture-content, but experiencing in the one instance a light-intensity of $\frac{1}{300}$, and in the other an intensity of $\frac{1}{25}$, were noted to react as follows: The leaves of the plants in the darker site gradually assumed a dark olive-green, were linear in shape, and measured on the average $2{\cdot}5 \times 0{\cdot}15$ inches, those of the plants in the lighter site were green-and-copper to entire copper (as in ***Fagus sylvatica*** var. *cuprea*), were narrowly lanceolate, and measured $4{\cdot}0 \times 0{\cdot}40$ inches on the average.

The foliage of the speçies is dimorphic: the *juvenile* leaves are *linear* (ranging from 2 to $5 \times 0{\cdot}1$ to $0{\cdot}4$ inches), with undulating, slightly crimpled margins; the *adults* are *broadly lanceolate to broadly elliptical* ($1{\cdot}5$ to $3{\cdot}5 \times 0{\cdot}75$ to $1{\cdot}5$ inches). Forms *intermediate* between the *juvenile* and the *adult* forms occur—thus the leaves of larger seedlings and saplings are *lanceolate*, while those of the pole stages are almost *broadly lanceolate*. It is of importance to note that the light-intensity has a marked influence on the form of the foliage. As is indicated in the instance of the two-year seedlings grown under light-intensities of $\frac{1}{300}$ and $\frac{1}{25}$ above described, the higher light-intensities favour the production of broader leaves. In the sapling and pole stages the same effect is produced. Saplings and poles experiencing the normal low light-intensities (from $\frac{1}{100}$ to $\frac{1}{125}$ at 15 to 20 feet, on an average)

show foliage more juvenile on the whole than do plants of the same general dimensions growing under higher illumination. The temperature, humidity, and soil-moisture conditions of the sites bearing the *more-juvenile-foliaged* and the *less-juvenile-foliaged* individuals have been studied by instruments, but have been found to be practically identical (*e.g.* such small differences as 1–3° F. in mean diurnal temperature, 1–3 per cent. in mean diurnal relative humidity, and 1–4 per cent. in mean weekly holard, exist), the sole efficient factor differing to an appreciable extent being that of light. The light-intensity data given on page 324 show that as the distance from the ground is increased the strength of the light too is increased—thus it is evident that the taller the stage of *Faurea* the stronger is the light it experiences. *This increase in light experienced is reflected in the broader, less-juvenile form of the leaves.*

The responses of cultures of *Faurea McNaughtonii* seedlings raised from seed under regulated intensities of light, the other important factors (humidity, temperature, wind (and therefore rate of evaporation), and holard and *pH* value of the soil solution) being equalised in the screens used for the experiments, have been studied quantitatively. The nature of the experiments and the principal results obtained are worthy of brief description.

In July 1924, 18 even-sized, practically even-weight seedlings were submitted to a light-intensity of $\frac{1}{40}$, and 18 plants of the same size and of practically the same weights were submitted to that of $\frac{1}{200}$. The other efficient factors experienced by the plants are described in the tabular statement on page 324. In July 1926 the cultures were removed from the screens, the seedlings being measured, weighed, oven-dried, and incinerated ; in addition portions of their foliage were studied microscopically. The mean responses shown by the cultures are given in the tabular statement on page 324.

A perusal of the response data reveals the fact that seedlings growing under close canopy are much less thrifty than those under moderate. (See Table, p. 324.)

A microscopic examination of the fresh foliage showed the following differences according to the light-intensity experienced :—

The plants in the darker screen showed thinner cuticle than those in the lighter ; their epidermal cells were considerably vertically-compressed, with weak wavy lateral walls, whereas those in the lighter screen exhibited normal-shaped cells with stout walls ; their palisade was one layer deep only, the cells being much vertically-compressed, and the chloroplasts small, while the palisade was two-layered and possessed larger chloroplasts in the plants in the lighter screen. Spongy-parenchyma was more abundant in the lighter screen, and sclereids were better developed and more numerous. Stomata were confined to the lower surfaces of the leaves in the lighter

screen, but were occasionally found on the upper surfaces in the darker; they were more numerous per unit area in the darker screen.

LIGHT-INTENSITY EXPERIMENTS: HABITAT CONDITIONS AND GROWTH RESPONSES.

Average light-intensity.	Average relative humidity. (diurnal.)	Average temperature. (F.)	Average holard provided. (dry-weight.)	*pH* kept at.	Average height. (inches.)	Average diameter at the collar. (mm.)	Average fresh-wt. (grms.)	Average dry-wt. (grms.)	Average ash-wt. (grms.)	Average number of leaves per plant.
[illegible]	80 per cent.	60°	35–40 per cent.	5·5	9·4	4·68	7·994 (439 per cent.)	3·477 (462 per cent.)	0·072 (514 per cent.)	46
[illegible]	81·5 per cent.	59·5°	35–40 per cent.	5·5	5·2	3·01	1·823 (100 per cent.)	0·752 (100 per cent.)	0·014 (100 per cent.)	33

(2) *Temperature.*

Within the Lilyvlei Forest the species experiences a mean annual temperature of 60° F. The mean monthly maxima very rarely exceed 80° F. and the mean monthly minima seldom drop below 45° F. The absolute maximum so far recorded is 102·75° F. and the absolute minimum 34° F. Frost is never experienced at Lilyvlei, but it has been found that experimental quadrats of the species formed on sites experiencing even moderate frosts several times per annum, have suffered severely.

The three- to six-months-old seedlings are liable to suffer severely from insolation-lesions (*vide* Toumey and Neethling, 1924) produced by high surface-soil temperatures. If the total soil-moisture (holard) at the surface drop below 3 per cent. (dry-wt.), and the temperature at the surface be 150° F. or greater, for more than half an hour, a waist-like constriction or *lesion* is formed at the collar of the seedling, death of the plant setting in shortly afterwards. Even strongly lignified ***Faurea*** plants of several years of age show signs of the constrictions after very dry, hot weather, their growth being slightly or totally inhibited on account of the reduced upward movement of water and solutes.

(3) ***Humidity.***

The humidity within the Lilyvlei Forest is usually high, ranging from 65 to 90 per cent. R.H. during the diurnal hours, according to nature of

exposure and nature of the current weather. During the blowing of the dry, warm Föhn-like " Bergwinds " (*vide* J. Phillips, 1926 (1)) from the north and north-west, however, the R.H. falls as low as 16–20 per cent., the temperature rising to values between 75° and 100° F. " Bergwinds," on account of their low humidity, are responsible for desiccation of the exposed, immature foliar shoots and immature leaves of *Faurea McNaughtonii*, and for the shrivelling of the young inflorescences and immature nuts.

Owing to their semi-sclerophyllous nature the adult leaves, even when exposed to severely low humidity and to high temperatures, do not show signs of discomfort.

(4) *Soil-moisture.*

The holard within the Lilyvlei Forest is not high, the superabundance of the water-filching *Trichocladus crinitus* layers, and the occurrence of a certain amount of Bokkeveld-derived soil overlying Table Mountain Sandstone and occasional Bokkeveld beds, allowing of drainage better than the normal, doubtless being responsible to some extent for this condition. The fact of the holard being *medium* instead of *high* is conducive to exceptionally fine growth of *Faurea* and other forest trees wherever the soil is sufficiently deep. The following are representative holard values for several depths in the better portions of the Lilyvlei Forest :—

Depth : Inches.	Nature of the soil.	Mean holard (on dry-weight).
2–3	Humus . . .	30 per cent.
6–9	Pale sandy loam . .	35 ,,
18–21	Darker sandy loam with a little clay . .	35 ,,
30–36	Clay, hot, heavy . .	41 ,,

In low-lying " kloofs " the conditions are naturally somewhat moister, the percentages being increased by about 5–10 per cent. at all depths.

The echard (non-available moisture-content) for the sandy loam of the Lilyvlei Forest and for the six-months-old seedlings of *Faurea McNaughtonii* is approximately 16 per cent., so, in periods of drought, critical moisture-contents are approached, with the results that growth is slightly inhibited for a period and that occasional plants (seedlings) succumb to drought.

The subject of response of the seedlings to soils of identical origin and nature supplied with definite amounts of moisture has been studied experimentally. Three cultures of seedlings of the same origin, age, dimensions, vigour, and practically of the same fresh-weight, were grown under identical

conditions of light, atmospheric humidity, temperature, exposure to wind, and *pH* value of the soil, *the sole efficient factor differing, culture by culture, being that of soil-moisture-content.*

The habitat conditions provided the cultures and the responses made by the latter, at the end of fourteen months, are described below. It is seen that the plants receiving a holard of approximately 50 per cent. are the finest in the series.

HOLARD EXPERIMENTS: HABITAT CONDITIONS AND GROWTH RESPONSES.

Average light-intensity.	Average relative humidity. (diurnal.)	Average temperature. (F.)	Average holard provided. (dry-wt.)	*pH* kept about.	Average height. (inches.)	Average fresh-wt. (grms.)	Average dry-wt. (grms.)	Average ash-wt. (grms.)	Average root length. (inches.)	Average number of leaves per plant.
$\frac{1}{15}$	77 per cent.	61·5°	20 per cent.	5·2	3·7	0·942 (100 per cent.)	0·546 (100 per cent.)	0·015 (100 per cent.)	8·5	18 (small)
,,	,,	,,	40 per cent.	5·1	6·0	2·650 (281 per cent.)	1·196 (219 per cent.)	0·048 (320 per cent.)	4·2	43 (medium sized)
,,	,,	,,	50 per cent.	5·0	5·0	2·894 (307 per cent.)	1·246 (227 per cent.)	0·049 (327 per cent.)	2·5 (tap) 5·5 (main laterals)	34 (largest)

(5) *Hydrogen-ion Concentration of the Soil Solution.*

Faurea McNaughtonii in the Lilyvlei Forest occurs on soils showing *high pH* values, and the reasons for the moderate degree of acidity existing in the soils of this forest doubtless reside in the facts that the holard is moderate only, and that occasional Bokkeveld beds and Bokkeveld-derived soils slightly richer in basic constituents occur. Numerous determinations of the *pH* values of moisture-regulated samples of soil from the Lilyvlei Forest have been made by means of E. T. Wherry's (1924) Double-wedge Comparator method.

It has been found that young regeneration of *Faurea* is absent from, or scarce in, soil showing values lower than *pH* 4·9 at depths of 2–6 inches, that soil bearing the most abundant and the best-developed regeneration shows values ranging from *pH* 5·3 to *pH* 5·0 at the same depths, and that in the *Faurea-other* spp. association the *pH* values at 18–24 inches range from 5·6 to 5·3, whereas in adjacent forest where *Faurea* is sub-dominant only, they lie between 4·9 and 5·1.

(6) *Biotic Factors.*

Apart from agents of pollination described under a separate section, there are no biotic factors of any importance influencing the species.

In isolated instances the fungus *Hysterostoma Faurea* Dge. (Polystomellaceae) causes loss of assimilating surface in adult leaves. No other diseases are known.

No organisms live in symbiosis with *Faurea McNaughtonii.*

Notes Concerning the Biology of the Flowers and Fruits.

(1) *Nature and Abundance of the Flowers.*

The zygomorphic, cream or faintly pink-tinted flowers are borne in terminal, solitary short-peduncled, cylindrical, dense 3–6 inch long spikes; the flowers number from 70 to over 150 per spike, but the average number, on the basis of thousands of counts, appears to be in the vicinity of 102. From collections of the *entire* inflorescence crops of a number of representative trees it is estimated that the average tree (from 11-inch diameter upward) annually bears just about 1000 spikes: that is, the average tree bears about 102,000 flowers. From further observations and from transect data it seems clear that about 2·06 trees per acre bear flowers—that is, the 1000-acre portion of Lilyvlei Forest possesses about 2060 " average " flower-producers.

The flowers are faintly scented in instances, in others they possess no scent of any kind.

(2) *Flowering and Fruiting Seasons.*

At the Knysna the tree in its *smaller-tree* and *adult-tree* stages produces an abundance of flowers once per year. Phenological observations, however, establish the fact that some trees do not flower *every* year, but may miss one year or several years. Such trees, it is to be noted, usually do not receive sufficient light, their crowns being covered by those of larger trees of *Faurea* or of other dominant species adjacent.

The flowering period lies between *early* March and *late* May, although some trees show flowers as late as *mid* or even *late* June.

In the Transkeian forests it seems that flowering seasons are irregular. In Natal, according to Forester Tustin, flowering takes place every year, but some years show much heavier crops than others.

For the Lilyvlei Forest the flowering and fruiting behaviour of the tree may be summarised as follows :—

Period.	Behaviour.
(1) Late February . .	First signs of inflorescence buds.
(2) Early March–late March	Development of the inflorescence axes and of the flower-buds thereon.
(3) Late March–mid April .	*First* flowers open in acropetal succession. Bird and insect pollinators appear in small numbers. *First* flowers are fertilised.
(4) Mid April–mid May .	*Main* flower crop opens; pollinators increase considerably. Fertilisation of *main* crop is accomplished. *First* flowers show *immature* fruits.
(5) Mid May–early June .	A few *late* flowers appear, few of these being fertilised, as the pollinators have decreased considerably. *First* flowers have produced *mature* fruits which mostly persist on the spikes.
(6) Mid June–mid July .	Bulk of fruits produced by *first* flowers fall, usually with the axes. *Main* flowers have produced small, *immature* fruits.
(7) Mid July–early August .	*Main* flower crop produces *mature* fruits.
(8) Early Aug.–late Aug. .	Most of fruiting spikes fall.
(9) October–late November	A few fruiting spikes produced by *late* flowers may appear on the trees.

(3) *Pollination.*

Observations have been carried out in the Lilyvlei Forest and at the Research Station, Deepwalls, employing *Faurea McNaughtonii* inflorescences arranged in various manners and an observation hive of *Apis mellifica.*

The only important pollinating agent is *Apis mellifica*, which seeks pollen and nectar. On account of the flower being *protandrous*, much pollen is lost, nevertheless a fair number of the flowers are self-pollinated. Ants and Diptera, seeking nectar, and Melolonthinae seeking, and to some extent destructive to, pollen, are responsible for the pollination of a few flowers only. The Sunbirds, *Cinnyris afer* and *C. chalybeus*, and the "White-eye," *Zosterops capensis*, are relatively unimportant agents of pollination, and are sometimes destructive to the flowers.

The degree of successful fertilisation achieved—on the basis of the proportion of flowers that develop to form fruits—is high: 41–80 per cent. of the flowers producing fruits. The only other spp. indigenous to the Knysna Forests attaining such a high percentage of success being *Cunonia capensis* and *Platylophus trifoliatus* (*vide* J. Phillips, 1926 (2)). This high figure of

success is the more surprising on account of the great loss of pollen through the flowers of ***Faurea*** being *protandrous*, and on account of the densely crowded nature of the spicate inflorescences.

It is of interest to observe that while the degree of successful fertilisation is high the *germinative capacity* (*i.e.* the proportion of *viable* seeds) is extremely low—ranging from $\frac{1}{2}$ to 1 per cent. Development of the embryo does not proceed beyond an immature stage, but the walls of the fruit develop in the normal manner. Fruits containing normal *mature* seeds cannot be distinguished externally from those containing *partially-developed* ones except by means of the balance.

(4) *The Fruits ; Their Nature and Dispersal.*

The fruit is a long-villous *nut*, about $\frac{1}{8}$ by $\frac{1}{4}$ inch, with a persistent style which ranges from $\frac{1}{2}$–1 inch in length and is four-angled and furrowed.

In transverse section it is seen that a ring of 10 vascular bundles, associated with which is a development of supporting sclerenchyma, surrounds the chamber containing the seed. The ground-tissue of the nut cover is parenchymatous, the outer margin showing a greenish band $\frac{1}{30}$ inch wide, followed by a line of brown from which springs a very dense growth of short, russet hairs giving the cover its reddish appearance.

Long, unicellular, air-filled hairs spring from the same band, these hairs varying from $\frac{1}{3}$–$\frac{1}{2}$ inch in length by 15–20μ. They point in the same general direction as the style—upward and outward.

The single fleshy seed is *exalbuminous* ; when mature and normally developed it measures $\frac{1}{7}$ by $\frac{1}{8}$ inch, being somewhat ovate. It is encased in a brown membrane which in turn is enclosed in a larger membranous sac. The seed is laterally seated, and the radicle points towards the base of the capsule.

On germination the capsule is borne above the ground by the broad cotyledons, the style pointing upward and outward ; it remains in position for several days only. The average period required for germination ranges from one and a half to three months ; *the capacity for lying dormant* is poor, the seeds decaying three to four months after their fall. About 1400 mature-seeded nuts weigh 1 ounce.

The germinative capacity, as ascertained from dissection of many thousands of nuts produced by many individuals in three different years, and from numerous germination tests under controlled conditions, is extremely low, ranging from $\frac{1}{2}$–1 per cent. As already pointed out, the *non-viable seeds are under-developed*, there being no signs of disease of any kind.

It has been stated above that the average flower-bearing capacity of *Faurea* in Lilyvlei Forest is about 102,000 flowers per tree. In the event of every one of these flowers being fertilised and developing to form a nut, the average number of viable seeds produced by a single tree would be small, ranging from 500–1000 only. Owing to strong winds and other natural agencies many of the *viable* and *non-viable* seeds fall *prematurely*, hence the number of *mature viable* seeds is further reduced. From quadrat studies it appears that approximately 40 per cent. of the *viable* seeds succeed in germinating and in establishing seedlings, *this comparatively high establishment figure being due to the absence of biotic foes harmful to either nut, seed, or seedling.*

The overwhelming majority of the nuts fall upon the *crown-influence-zone* of the parent trees. As many as 2000 nuts per square metre are to be found under many larger trees. The *long hairs* described as being borne by the walls of the nut *do not assist in dispersal by wind*, as they are too fine and too few, to offer any resistance to the air.

Nuts containing viable seeds have been dropped from various heights under canopy in the Lilyvlei Forest, and it has been found that when there is absolutely no breeze, such nuts take approximately $1\frac{3}{8}$ seconds (per stop-watch) to fall 20 feet, provided no shrubs inhibit their downward passage. There is no tendency for the nuts to hang even for a few seconds in the air. During winds of forces 1, 2, and 3 on the *Beaufort Scale* (*i.e.* of velocities 2–5, 6–11, and 12–18 *feet per second* respectively) the nuts take approximately 2–3·5 seconds to fall the same distance, and during winds of forces 4 and 5 (*i.e.* of velocities 19–27, and 28–36 *feet per second* respectively) the time taken ranges from 4–8 seconds. Force 6 winds (*i.e.* of velocity 37–46 *feet per second*) have been noted to waft the nuts not more than a few yards beyond the *crown-influence-zones* of the parents. Nuts dropped from heights of 50 and 25 feet on fully exposed sites during winds of various velocities have always failed to find their way more than a few yards from the base of the ladder from which they were dropped. *The dispersal mechanism is of extremely low efficiency.* In Nature many of the nuts do not fall *singly* from the axes of the spikes, but the *entire* fruiting spikes fall, the result being that even the slight influence of the wind in dispersal is entirely prevented from acting.

The nuts are eaten neither by birds nor mammals, nor are they borne even short distances by insects. Water is an inefficient agent of dispersal, as the dampened hairs of the nut attach themselves to various obstacles upon the ground and thus inhibit the passage of the nut.

From experiments it has been found that strongly flowing water of the *run-off* (*i.e.* the water that does not enter the soil during periods of rain) may bear the nuts for distances of several dozen yards, but it is extremely

doubtful whether any of the nuts find their way to the smaller streams or to the rivers within the Lilyvlei Forest, for careful search along the beds of such courses has always failed to reveal the presence of a single fruit.

Natural regeneration, owing to the poor means of dispersal, *is aggregated on the crown-influence-zones* of the parent trees, thus a steady increase in the local stocking of *Faurea McNaughtonii* is taking place. At the same time the gradual extension of the limits of the *Faurea McNaughtonii-other* spp. association is being brought about, for the tendency is for some of the regeneration, just outside the *crown-influence-zone* of the marginal trees, to grow up into trees that in turn produce young plants just beyond the cover of their crowns. While the *mean absolute frequency* of plants under 15 feet in height has been stated to be 1·1 per square yard, it is necessary to point out that under many of the parent trees thriving, richly stocked societies of seedlings of all stages occur, some of these societies showing as many as 50–100 cotyledon-stage and one- to two-year-old plants per square yard.

The *mortality* is high owing to the competition for moisture, solutes, and growing-space itself, but despite this, the number of large seedlings and saplings in many such local societies is large.

The Discontinuous Distribution of *Faurea McNaughtonii*: A Possible Explanation.

The peculiar distribution of *Faurea McNaughtonii* has long been of interest to South African forest officers, so the following, admittedly highly imperfect, possible explanation of the matter may prove worthy of their attention.

When the distribution of the species of the genus *Faurea* is studied it is seen that there are at least two *wide-ranging* (the " wides " of Willis : 1922) species, two species with *discontinuous, widely-separated centres of occurrence*, and seven species and one variety which are practically endemic to quite small areas, thus :

[Table.

Species.	General distribution. (For details *vide* the works of T. Dyer, Kotze, and E. P. Phillips in the list of references.)	Remarks.
(1) F. speciosa Welw.	Transvaal; Angola; Mozambique (British East and Central Africa).	Wide ranging.
(2) F. saligna Harv. .	Transvaal; Angola; Natal and Zululand; S. Rhodesia; (Mozambique ?).	Wide ranging.
(3) F. McNaughtonii Phill. . .	Mariep's Kop (Transvaal), teste J. D. Keet; Ngomi (Zululand); the W. and E. Pondoland Forests; Gouna (Knysna).	Distribution discontinuous.
(4) F. discolor Welw. .	Angola (between Lopollo and Nene); Mozambique; (Uhehe; Montanana).	"
(5) F. racemosa Farm.	Mozambique district only: Mt. Mlanje.	Endemic to small area.
(6) F. Wentzeliana Engl. . .	East Africa: Kinga Mtns.	"
(7) F. usambarensis Engl. . .	Usambara: between Heboma and Mbalu.	"
(8) F. dicipiens. . .	Nyassaland; Shire Highlands.	"
(9) F. discolor var. Cyclolepra Hiern.	Angola district only: Nene.	"
(10) F. intermedia Engl. and Gilg. . .	Angola district only: above Kohi.	"
(11) F. Galpini Phill. .	Transvaal only: Barberton, Lydenberg, Zoutpansberg districts.	"
(12) F. forficuliflora, J. G. Baker (1883: 243). . .	Madagascar only: Imerina Province.	Endemic to a very small area.

From the point of view of Willis (1922) it would seem as if one, other, or both of the wide-ranging species, *F. speciosa* and *F. saligna*, had given rise to the species with more limited range on encountering, in the course of their migrations, environmental conditions markedly different from those to which they were accustomed. At all events the massing of four endemics in the Mozambique district on the east, of two endemics in Angola on the west, and of one endemic in the Transvaal is suggestive of this having taken place. (The Madagascar endemic possibly may have been formed during

the probable temporary reunion of Madagascar and continental Africa in Miocene times.)

If such an hypothesis be held one might suggest that either *F. speciosa* or *F. saligna* gave rise to *F. McNaughtonii* at Mariep's Kop, and that *F. saligna* was the form from which *F. McNaughtonii* originated at Ngomi, Natal. Assuming the aforementioned suppositions to be correct, the occurrence in the Transkeian Forests and at Gouna, Knysna, of *F. McNaughtonii* is yet unexplained. Migration westward from Ngomi can scarcely be advocated as being the process responsible, for not only is it a long distance, over country mostly unfavourable to the establishment of the species, from Ngomi to the St. John's district (Nenga Forest), and from the Elliotdale district (Cwebe Forest) to Gouna, but also the centres of occurrence within the Transkeian Forests are far separated. In addition there are no traces of the species in the forests separating these several centres. Death of the tree in the intervening areas, on account of its being an *effete* species, cannot be considered to throw any light on the subject, for despite the low germinative capacity and the poor migration of the germules, sufficient regeneration must have been produced to assure the continued establishment of the species.

The *polygenesis* hypothesis (*vide* Engler, 1879 ; Clements, 1904)—whereby one species or several species, in the same or in different areas, at the same or at different times, is or are conceived as giving rise to a new species—offers some slight assistance. Possibly *F. McNaughtonii*, within the Transkeian and the Gouna Forests, originated from a still-existing or now extinct Proteeacous plant common to both regions, or possibly two different but closely related Proteaceous species were responsible for the origin of *F. McNaughtonii* in the different regions.

How long it is since *F. McNaughtonii* first appeared at Gouna it is obviously impossible to say with any certainty, but it seems clear from a knowledge of the present distribution of the tree in that locality and from a study of its migration, germination, and establishment characteristics, that the species has been in the locality for several thousand years at least.

On the whole the writer is inclined to the view that the " wides " *F. speciosa* and *F. saligna* and *polygenesis* or " multiple origin " both have contributed to the moulding of the species *F. McNaughtonii*, and are jointly responsible for its sporadic occurrence.

In conclusion let it be said that from a study of the behaviour of the species in the Lilyvlei Forest, Gouna, and from a knowledge of the topographic and other habitat conditions obtained therein, there can be no doubt that the species is gradually extending its limits. The definite marking of outlying trees and a clear description of their positions topographically and

sociologically, to-day, will aid a later generation of botanists to decide what the actual increase in range has been in say a century or more.

Acknowledgments.

The writer is indebted to Conservators Doran (Transkei), Boocock (Natal), and Keet (Transvaal) for kindly placing information concerning the *F. McNaughtonii* in their Conservancies at his disposal, and to Mr. A. P. D. McLean who, through the kind services of Dr. E. P. Phillips, supplied references concerning the distribution of the tropical African spp. of *Faurea*.

The whole of the work has been done under the direction of the Chief Conservator of Forests, Pretoria.

Summary.

Faurea McNaughtonii Phill. ("Terblanz"), a large Proteaceous tree, occurs in a single area of about 1000 acres, Lilyvlei Forest, Gouna Forest Reserve, Knysna; it is also recorded from several isolated centres in the Elliotdale, Lusikisiki, and St. John's districts, from Ngomi Forest, Northern Natal, and from Mariep's Kop, Transvaal.

At Gouna there are about 12,000 trees above 1-inch diameter at breast-height, and on the 1000-acre portion the *absolute frequency* of plants under 15 feet in height and 1-inch diameter, is 1·1 per square yard. The *percentage frequency* of *Faurea* above 1-inch diameter on the 1000-acre portion is 2·61 per cent. The tree occurs as a *dominant* in small associations termed the *Faurea McNaughtonii-other* spp. associations, the *co-dominants* being *Podocarpus Thunbergii* Hook. and *Olea laurifolia* Lamk. It is, however, more generally found as a *sub-dominant* in the extensively developed *Podocarpus Thunbergii-Olea laurifolia-other* spp. association.

In the Transkei and in Natal the tree is less locally abundant, and is not a dominant in any community.

The prime factors of the habitat in so far as they influence the species have been studied in the Lilyvlei Forest and under controlled conditions at the Research Station, Deepwalls, Knysna. Summarising, the species is *moderately light-demanding*, growing best under intensities ranging from $\frac{1}{40}$ to $\frac{1}{8}$ of full sunlight, but is *insolation-tender* in early youth; (the leaves are dimorphic, the juvenile forms remaining longer in position where the light-intensity is low); young foliar shoots are very susceptible to desiccation by winds of *low humidity* (16–20 per cent.); *the average holard* at 18–21 inches in Lilyvlei Forest is 35 per cent. (on the dry-weight), the figure for the 6–9 inches depth being 35 per cent. also, and that for the 2–3 inches depth,

30 per cent. ; (while young regeneration is abundant and well developed on soil of holard 30 per cent., it has been found experimentally that growth is better when the holard is raised to 40–50 per cent.) ; the *echard* for the regeneration of the species in the sandy loams of the Lilyvlei Forest has been fixed at 16 per cent. (on dry-weight) ; *soil of low* pH *value* (below *pH* 4·7) is not occupied by regeneration even when parent trees are well represented.

Flowers are produced annually by most of the trees—there being about 2060 of the 12,000 trees and poles that actually flower—but some trees may miss one year or several years. It is estimated on the basis of various counts that the average number of flowers produced by a tree is about 102,000. The main flowering takes place between mid April and mid May, but the general season extends from early March to late June. Pollination is principally effected by *Apis mellifica*, although a large number of flowers are self-pollinated ; the degree of pollination for which the birds *Cinnyris* spp. and *Zosterops capensis* are responsible is insignificant. The degree of successful fertilisation achieved (on the basis of the number of flowers that develop to form nuts), is high, 41–80 per cent. ; the only other spp. at the Knysna approaching such a figure being *Cunonia capensis* and *Platylophus trifoliatus*.

The fruit is a single-seeded, long-villous nut. The seed is ex-albuminous, and takes one and a half to three months to germinate, its capacity for lying dormant being low. Germination experiments show that the *germinative capacity* is ½–1 per cent. only, the reason being the under-development of the seeds, there being no biotic or physiological diseases known.

Dispersal of the nuts is over very short distances, the long hairs being very inefficient aids to flight ; water and animals scarcely disperse the germules, the result being the *aggregation of regeneration* on the *crown-influence-zones* of the parents.

The discontinuous distribution of the species is considered, it being held that the wide-ranging species *Faurea speciosa* and *F. saligna* have been responsible for the appearance of *F. McNaughtonii* in the Transvaal and in Natal, and that the occurrences of the latter species in the Transkei and at Gouna are due to *polygenesis* having taken place.

It is held that the species is extending its limits gradually at Gouna.

A 200-acre portion of the Forest of Lilyvlei, Gouna, has been set aside by the Forest Department as a scientific reserve.

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NOTE ON HYPERORTHOGONANTS.

By Sir Thomas Muir, F.R.S.

1. Sylvester's suggested generalisation of the original conception of an orthogonant, although neglected for a generation, has, since Hadamard recalled it to notice in 1893, received considerable attention: and its properties are now readily ascertainable by the student. The same does not hold in regard to a second generalisation (the *hyperorthogonant*) which is of quite a different type, and which not improbably may prove the more important of the two. Hence the present initiatory Note.

2. A determinant whose elements are complex and which is such that its complex conjugate is its determinantal reciprocal is appropriately named a *hyperorthogonant*: for example, if

$$\begin{vmatrix} a_1 & a_2 & a_3 \\ \beta_1 & \beta_2 & \beta_3 \\ \gamma_1 & \gamma_2 & \gamma_3 \end{vmatrix} \overset{r}{\underset{r}{\times}} \begin{vmatrix} \bar{a}_1 & \bar{a}_2 & \bar{a}_3 \\ \bar{\beta}_1 & \bar{\beta}_2 & \bar{\beta}_3 \\ \bar{\gamma}_1 & \bar{\gamma}_2 & \bar{\gamma}_3 \end{vmatrix} = \begin{vmatrix} 1 & . & . \\ . & 1 & . \\ . & . & 1 \end{vmatrix},$$

then $|a_1\beta_2\gamma_3|$ is a hyperorthogonant.

Evidently, if Ω be a hyperorthogonant, then $\bar{\Omega}$ is so also.

3. *If Ω be a hyperorthogonant and $\bar{\Omega}$ its complex conjugate, then the product of any element of Ω by $\bar{\Omega}$ is equal to the cofactor of the corresponding element in $\bar{\Omega}$.*

Taking the first three of the nine given equations included in the definition of Ω, namely

$$\begin{aligned} a_1\bar{a}_1 &+ a_2\bar{a}_2 + a_3\bar{a}_3 = 1 \\ a_1\bar{\beta}_1 &+ a_2\bar{\beta}_2 + a_3\bar{\beta}_3 = 0 \\ a_1\bar{\gamma}_1 &+ a_2\bar{\gamma}_2 + a_3\bar{\gamma}_3 = 0, \end{aligned}$$

and using on them the multipliers

$$|\bar{\beta}_2\bar{\gamma}_3|, \quad |\bar{\gamma}_2\bar{a}_3|, \quad |\bar{a}_2\bar{\beta}_3|$$

respectively, we have by addition

$$a_1 |\bar{a}_1\bar{\beta}_2\bar{\gamma}_3| + a_2 \cdot 0 + a_3 \cdot 0 = |\bar{\beta}_2\bar{\gamma}_3|.$$

Similarly from the next three given equations with the same set of multipliers we obtain

$$\beta_1 \; | \bar{a}_1\bar{\beta}_2\bar{\gamma}_3 | \; + \; \beta_2 \cdot 0 \; + \; \beta_3 \cdot 0 \; = \; | \bar{\gamma}_2\bar{a}_3 |,$$

and from the last three given equations

$$\gamma_1 \; | \bar{a}_1\bar{\beta}_2\bar{\gamma}_3 | \; + \; \gamma_2 \cdot 0 \; + \; \gamma_3 \cdot 0 \; = \; | \bar{a}_2\bar{\beta}_3 |.$$

The theorem is thus proved true for any element of the first column of Ω. Similarly we can prove it for any element of the second column by using the multipliers

$$| \bar{\beta}_3\bar{\gamma}_1 |, \quad | \bar{\gamma}_3\bar{a}_1 |, \quad | \bar{a}_3\bar{\beta}_1 |,$$

and for any element of the third column by using

$$| \bar{\beta}_1\bar{\gamma}_2 |, \quad | \bar{\gamma}_1\bar{a}_2 |, \quad | \bar{a}_1\bar{\beta}_2 |.$$

4. *If the multiplication of a hyperorthogonant by its complex conjugate be performed in column-by-column fashion, the result is exactly the same as when it is done row-wise.*

We have just seen in § 3 that

$$\begin{aligned} a_1 \; | \bar{a}_1\bar{\beta}_2\bar{\gamma}_3 | \; &= \; | \bar{\beta}_2\bar{\gamma}_3 |, \\ \beta_1 \; | \bar{a}_1\bar{\beta}_2\bar{\gamma}_3 | \; &= \; | \bar{\gamma}_2\bar{a}_3 |, \\ \gamma_1 \; | \bar{a}_1\bar{\beta}_2\bar{\gamma}_3 | \; &= \; | \bar{a}_2\bar{\beta}_3 |, \end{aligned}$$

and, using on these the multipliers

$$\bar{a}_1, \quad \bar{\beta}_1, \quad \bar{\gamma}_1$$

respectively, we have by addition

$$| \bar{a}_1\bar{\beta}_2\bar{\gamma}_3 | \cdot (a_1\bar{a}_1 \; + \; \beta_1\bar{\beta}_1 \; + \; \gamma_1\bar{\gamma}_1) \; = \; | \bar{a}_1\bar{\beta}_2\bar{\gamma}_3 |,$$

and therefore

$$a_1\bar{a}_1 \; + \; \beta_1\bar{\beta}_1 \; + \; \gamma_1\bar{\gamma}_1 \; = \; 1.$$

Similarly the multipliers $\bar{a}_2$, $\bar{\beta}_2$, $\bar{\gamma}_2$ are seen to lead us to

$$a_1\bar{a}_2 \; + \; \beta_1\bar{\beta}_2 \; + \; \gamma_1\bar{\gamma}_2 \; = \; 0,$$

and the multipliers $\bar{a}_3$, $\bar{\beta}_3$, $\bar{\gamma}_3$ to

$$a_1\bar{a}_3 \; + \; \beta_1\bar{\beta}_3 \; + \; \gamma_1\bar{\gamma}_3 \; = \; 0.$$

We thus have the first three of the nine required results : and, evidently, the two other triads are obtainable on starting with

$$\left.\begin{array}{l} \alpha_2 \,|\, \bar{\alpha}_1\bar{\beta}_2\bar{\gamma}_3 \,| \;=\; |\, \bar{\beta}_3\bar{\gamma}_1 \,| \\ \beta_2 \,|\, \bar{\alpha}_1\bar{\beta}_2\bar{\gamma}_3 \,| \;=\; |\, \bar{\gamma}_3\bar{\alpha}_1 \,| \\ \gamma_2 \,|\, \bar{\alpha}_1\bar{\beta}_2\bar{\gamma}_3 \,| \;=\; |\, \bar{\alpha}_3\bar{\beta}_1 \,| \end{array}\right\} \quad \text{and} \quad \left\{\begin{array}{l} \alpha_3 \,|\, \bar{\alpha}_1\bar{\beta}_2\bar{\gamma}_3 \,| \;=\; |\, \bar{\beta}_1\bar{\gamma}_2 \,| \\ \beta_3 \,|\, \bar{\alpha}_1\bar{\beta}_2\bar{\gamma}_3 \,| \;=\; |\, \bar{\gamma}_1\bar{\alpha}_2 \,| \\ \gamma_3 \,|\, \bar{\alpha}_1\bar{\beta}_2\gamma_3 \,| \;=\; |\, \bar{\alpha}_1\bar{\beta}_2 \,| \end{array}\right.$$

respectively.

5. *If the column-by-column product of a hyperorthogonant* Ω *by any determinant* A *be* B, *then the row-by-column product of* $\bar{\Omega}$ *by* B *is* A.

By the datum $\qquad \Omega \overset{c}{\underset{c}{\times}} \mathrm{A} = \mathrm{B},$

i.e. $\qquad \Omega' \overset{r}{\underset{c}{\times}} \mathrm{A} = \mathrm{B},$

$$\therefore \qquad \bar{\Omega} \overset{r}{\underset{c}{\times}} \left\{ \Omega' \overset{r}{\underset{c}{\times}} \mathrm{A} \right\} = \bar{\Omega} \overset{r}{\underset{c}{\times}} \mathrm{B}.$$

But row-by-column multiplication is commutative,

$$\therefore \qquad \bar{\Omega} \overset{r}{\underset{c}{\times}} \Omega' \overset{r}{\underset{c}{\times}} \mathrm{A} = \bar{\Omega} \overset{r}{\underset{c}{\times}} \mathrm{B},$$

$$\text{i.e.} \qquad \bar{\Omega} \overset{r}{\underset{r}{\times}} \Omega \overset{r}{\underset{c}{\times}} \mathrm{A} = \bar{\Omega} \overset{r}{\underset{c}{\times}} \mathrm{B},$$

$$\therefore \qquad \mathrm{A} = \bar{\Omega} \overset{r}{\underset{c}{\times}} \mathrm{B}.$$

6. *The product of any minor of a hyperorthogonant* Ω *by* $\bar{\Omega}$ *is equal to the cofactor of the corresponding minor in* $\bar{\Omega}$.

Taking ω_{rs}, Ω_{rs} for the typical elements of Ω and its adjugate respectively, and making use first of § 3 above and then of Jacobi's theorem regarding a minor of the adjugate, we have

$$\bar{\Omega}^k . \begin{vmatrix} \omega_{11} & \omega_{12} & \cdots & \omega_{1k} \\ \omega_{21} & \omega_{22} & \cdots & \omega_{2k} \\ \cdots & \cdots & \cdots & \cdots \\ \omega_{k1} & \omega_{k2} & \cdots & \omega_{kk} \end{vmatrix} = \begin{vmatrix} \bar{\Omega}\omega_{11} & \bar{\Omega}\omega_{12} & \cdots\cdots & \bar{\Omega}\omega_{1k} \\ \bar{\Omega}\omega_{21} & \bar{\Omega}\omega_{22} & \cdots\cdots & \bar{\Omega}\omega_{2k} \\ \cdots & \cdots & \cdots & \cdots \\ \bar{\Omega}\omega_{k1} & \bar{\Omega}\omega_{k2} & \cdots\cdots & \bar{\Omega}\omega_{kk} \end{vmatrix}$$

$$= \begin{vmatrix} \bar{\Omega}_{11} & \bar{\Omega}_{12} & \cdots\cdots & \bar{\Omega}_{1k} \\ \bar{\Omega}_{21} & \bar{\Omega}_{22} & \cdots\cdots & \bar{\Omega}_{2k} \\ \cdots & \cdots & \cdots & \cdots \\ \bar{\Omega}_{k1} & \bar{\Omega}_{k2} & \cdots\cdots & \bar{\Omega}_{kk} \end{vmatrix}$$

$$= \bar{\Omega}^{k-1} \begin{vmatrix} \bar{\omega}_{k+1,k+1} & \cdots\cdots & \bar{\omega}_{k+1,n} \\ \cdots & \cdots & \cdots \\ \bar{\omega}_{n,k+1} & \cdots\cdots & \bar{\omega}_{n,n} \end{vmatrix}$$

and therefore

$$\bar{\Omega} \cdot |\, \omega_{11} \ldots \omega_{kk} \,| = |\bar{\omega}_{k+1,k+1} \ldots\ldots \bar{\omega}_{nn} \,| ,$$

as was to be proved.

7. *If each* k-*line minor formable from any array of* k *rows of* Ω *be multiplied by the corresponding minor of* $\bar{\Omega}$, *the sum of the products so obtained is equal to* 1.

From the theorem of the preceding paragraph by means of multiplication and addition

$$\bar{\Omega}\cdot\sum \mid \omega_{11}\ .\ .\ .\ \omega_{kk} \mid \mid \bar{\omega}_{11}\ .\ .\ .\ \bar{\omega}_{kk} \mid \ = \ \bar{\Omega},$$

whence by division there comes the desired result.

8. *If* P *be any determinant of the same order as the hyperorthogonant* Ω, *then the sum of the diagonal elements of the product* $\Omega \mathrm{P} \bar{\Omega}'$ *is equal to the corresponding sum in* P.

If P be $\mid l_1 m_2 n_3 \mid$ and Ω be $\mid a_1 \beta_2 \gamma_3 \mid$, we know by a property of bipartite functions that the sum of the principal elements of the product $\Omega \mathrm{P} \bar{\Omega}'$ is equal to

$$\begin{array}{ccc|c} a_1 & a_2 & a_3 & \\ \hline l_1 & l_2 & l_3 & \bar{a}_1 \\ m_1 & m_2 & m_3 & \bar{a}_2 \\ n_1 & n_2 & n_3 & \bar{a}_3 \end{array} \quad + \quad \begin{array}{ccc|c} \beta_1 & \beta_2 & \beta_3 & \\ \hline l_1 & l_2 & l_3 & \bar{\beta}_1 \\ m_1 & m_2 & m_3 & \bar{\beta}_2 \\ n_1 & n_2 & n_3 & \bar{\beta}_3 \end{array} \quad + \quad \begin{array}{ccc|c} \gamma_1 & \gamma_2 & \gamma_3 & \\ \hline l_1 & l_2 & l_3 & \bar{\gamma}_1 \\ m_1 & m_2 & m_3 & \bar{\gamma}_2 \\ n_1 & n_2 & n_3 & \bar{\gamma}_3 \end{array}$$

But in this the cofactor of $l_1 = a_1\bar{a}_1 + \beta_1\bar{\beta}_1 + \gamma_1\bar{\gamma}_1 = 1,$
and the cofactor of $m_2 = a_2\bar{a}_2 + \beta_2\bar{\beta}_2 + \gamma_2\bar{\gamma}_2 = 1,$
and the cofactor of $n_3 = a_3\bar{a}_3 + \beta_3\bar{\beta}_3 + \gamma_3\bar{\gamma}_3 = 1,$

and the cofactor of any other element of the repeated square array is 0. Therefore the sum in question is equal to

$$l_1 + m_2 + n_3$$

as affirmed.

9. When the foregoing theorems are specialised by making all the cofactors of $\sqrt{-1}$ vanish, the results reached are the well-known initial properties of the ordinary orthogonant. Other properties less familiar are doubtless derivable in the same way from generalised analogues of the like type.

10. So far as I have been able to learn use was first made of a hyperorthogonant in a paper by Petrini in 1901. A few months later in the same year they appeared in a more notable paper by Autonne, and then not till 1909 when they were used by Schur. The last writer knew of Autonne's work, but neither he nor Autonne refer to Petrini.* In 1910 they were

* Petrini, H.—"Nota sobre la transformacion ortogonal de una determinante," Revista trim. de Mat., pp. 11–15.

Autonne, S.—"Sur l'hermitien," Rendic. del Circ. Mat., pp. 104–128.

Schur, I.—"Ueber die characteristischen Wurzeln einer linearen Substitution, mit einer Anwendung auf die Theorie der Integral Gleichungen," Math. Annalen, lxvi, pp. 488–510.

first given their proper niche in a brief general account of orthogononal substitutions, the innovator being A. Loewy, who had been entrusted with the writing of the second chapter of the enlarged German edition of Pascal's Repertorium.*

RONDEBOSCH, S.A.,
24th January 1927.

* Repertorium der höheren Mathematik, Band I, Analysis, pp. 133–135. Loewy's references to himself and Frobenius should be noted.

DESCRIPTION OF A NEW SPECIES OF *XENOPUS* FROM THE CAPE PENINSULA.

By W. Rose and J. Hewitt.

(With Plate XVI.)

Suspicion that there might be a second species of *Xenopus* on the Cape Peninsula was aroused by the discovery during March 1925 of a single specimen that appeared to be distinct from the well-known and widely spread *laevis*. To this example, found about six inches down on the site of a temporary vlei, brief reference has already been made as follows *: "Apropos of this specimen, I suggest with all reserve the possibility of there being another species of *Xenopus* on the Flats. This specimen (and a dozen others found since) in my opinion differed from the normal on the following points: Nose sharper, teeth much longer, hind limbs proportionately longer, feet not quite so fully webbed, eyes smaller, tentacles not apparent, and, lastly, having in the mouth a peculiar organ that could most appropriately be described as having the appearance of a posteriorly attached tongue or a deflated air-sac. The stomach was brownish.

"*Length*.—Snout to vent 56 mm., nose to toe 120 mm."

Systematic search was made for further examples as opportunity permitted, and one or two were obtained from other parts of the Cape Flats. In February 1926, amongst some 400 individuals of *X. laevis* taken in the shallow Sylvermyn River, four distinctive juveniles of the new species were found; and later, largely through the assistance of a local naturalist, Mr. B. Peers, about a dozen adults were obtained from the same neighbourhood. These were found buried in a sandy hollow—becoming in winter a small pool—a few yards from the river, a few large examples of *laevis* being associated with them.

These various specimens have enabled us definitely to announce the occurrence of a hitherto unknown species in the Cape Peninsula; and we have pleasure in naming this novelty *Xenopus gilli*, in recognition of the unfailing assistance offered to us at the South African Museum by the Director, Dr. E. L. Gill, and his staff.

X. gilli appears to be less essentially aquatic than *laevis*; it can leap

* Annals of the South African Museum, vol. xx, 1926, p. 443.

with greater agility, but in demeanour is far more gentle and less boisterous, submitting to capture and handling with a higher degree of resignation and with little or no exudation of slime. The latter characteristic was well demonstrated when killing subjects in weak chloroform water: *laevis* became speedily covered by a thick layer of exuded slime, little or none being apparent in the case of *gilli*. It was also noted that whilst *laevis* died in more or less spread-eagled form, *gilli* invariably succumbed with the head depressed, the arms tight to the sides, and the back very strongly humped.

In living specimens the colour is as follows: dorsally—in light surroundings—a light brown with darker blotches, more or less symmetrically arranged on either side of a fairly definite vertebral streak; on the hind limbs the blotches are small, isolated, and somewhat stellate. In dark surroundings the colour is very much darker, but the markings are still discernible. Ventrally the colour is a pale yellow or yellow-brown, gradually darkening to deep yellow on the hind limbs; with puce spots, small and numerous on the throat, larger and fewer on the sides and hind limbs, and often quite absent from the centre of the belly.

The fully adult female measures from 50 to 55 mm. from nose to vent. The only voice of *Xenopus*, a very faint "Te te te," is, in my observation (W. R.), heard much more plainly and frequently from *gilli* than from *laevis*. Up to the present no tadpoles definitely referable to *gilli* have been secured.

Xenopus gilli sp. nov.

Description based on four adult specimens collected near Cape Town by Mr. Walter Rose. The type, an adult male, is in the Albany Museum, Grahamstown.

The species resembles *X. laevis* Daud., but differs as follows: fewer teeth, snout more pointed and projecting, subocular tentacle quite absent, toes relatively shorter, hind-limb more strongly granulated, anal flaps rather larger, ventral surfaces with black spots, smaller bodily size.

Head narrow, much narrower than the body, not strongly flattened; snout acutely rounded and projecting beyond the mandibular symphysis; upper jaw with about 24 teeth on each side, those in front largest, between the two series a distinct interval; no vomerine teeth; no trace of subocular tentacle; cuticle smooth throughout except for granulation on the hind-limb, the granules, which are white and easily visible to the naked eye, being scattered indefinitely over the hinder and upper surfaces of the leg and tarsus, becoming more numerous and closer together on the soles and under the basal joints of the two outer digits; inner metatarsal tubercle small or very small. Calcaneum decidedly longer than fourth metatarsal.

Anal lobes of female prominent. Nuptial asperities of male restricted to the inner side of the fore-limbs as in *laevis*, but whereas in the latter species the modified area is very much wider under the fore-arm than under the arm, in *gilli* the two areas are nearly of equal width. On each side of the breast and body, and especially in the axils, the skin is minutely and closely roughened, but this is only noticeable under a lens, the area being without dark pigmentation. In the male the skin of the foot ventrally is minutely and closely granulated throughout.

Colour pattern quite distinctive; ventral surfaces throughout with innumerable blackish spots of small or moderate size and variable shape; dorsal surface of male dark grey, with a few large darker blotches over the back, and small blotches of irregular shape over the hind-limb; two of the former are a symmetrical pair of elongated shape extending backwards from the interocular region to a point above the shoulders, and another but smaller pair occurs just in front of the vent; in the female the anterior pair is well marked, each blotch narrowing gradually in front to a point on the inner side of the eye and widening out behind, and between the two blotches there remains a pale mid-dorsal band with irregular or dentated margins, this band being distinguishable only over the first half of the body; no other blotches are traceable in female specimens. The hind-limb being carried forward, the tarso-metatarsal articulation extends beyond the end of the snout in the male, slightly in front of the eye in females.

Measurements.—Total length, M. 34 mm., F. 52 mm.; breadth at gape, M. 9, F. 12·5; length of hind-limb, M. 45, F. 64; length of calcaneum, F. 11, of fourth metatarsal, F. 8·5.

The pectoral girdle of *X. gilli* is more or less like that of *laevis*, but there are minor differences: *gilli* is less extensively arciferous, the cartilages overlapping only for a short distance immediately opposite the basal ends of the coracoids, whereas in *laevis* overlapping occurs for some distance anterior thereto along the bar joining the two main portions of the epicoracoid. It may be noted also that overlapping may occur from either side. In the girdle character, *gilli* somewhat approaches the firmisternous species *tropicalis* as known to us from a single specimen collected at Medje, Belgian Congo (American Mus. Nat. Hist.), but *tropicalis* is peculiar in that the epicoracoids are ossified (or strongly calcified); on the other hand, *mulleri* from Faradje, Belgian Congo (American Mus. Nat. Hist.), is distinctly arciferous in the region between precoracoid and epicoracoid, differing, however, from *laevis* in that the true left side overlaps (for a good account and figure of condition in *laevis*, see Professor C. de Villiers' paper in Annals of the Transvaal Museum, vol. x, 1924, pp. 197–211).

Another point of agreement between *tropicalis* and *gilli* lies in the relative proportions of the tarsal and metatarsal regions; on the other

hand, *laevis* and *mulleri* have more elongated metatarsals, the calcaneum and fourth metatarsal being about of equal width in *laevis*. In the colour pattern of the dorsal surface there is further indication of affinity with *tropicalis* of the Congo rain-forest ; but the two are well separated on the characters of the ocular tubercle and of the metatarsal tubercle, characters which impart a superficial resemblance to *laevis*.

We conclude that *gilli* and *tropicalis* are closely related species ; they bear somewhat the same relationship to each other as does *laevis* to *mulleri*. Whether the simplicity of *laevis* and *gilli* as compared with their tropical allies can be regarded as primitive or degenerate remains undecided. Yet, so far as the ocular tubercle is concerned, its fate in the Urodeles seems to show that the condition in *gilli* should be accepted as primitive if the following assumptions are conceded : that the Aglossa, like other Anura, were originally to some extent terrestrial ; and that an organ may not experience the phenomenon of reversible evolution.

It is interesting to notice that *X. clivii* from Erythraea is also characterised by the possession of a short subocular tubercle like that of *laevis*, so that the Central African species, with long tentacles, are flanked both on north and south sides by species with short or obsolete tentacles. This seems easily explicable on the hypothesis of increased structural developments in the better watered and warmer regions as the species become more completely aquatic.

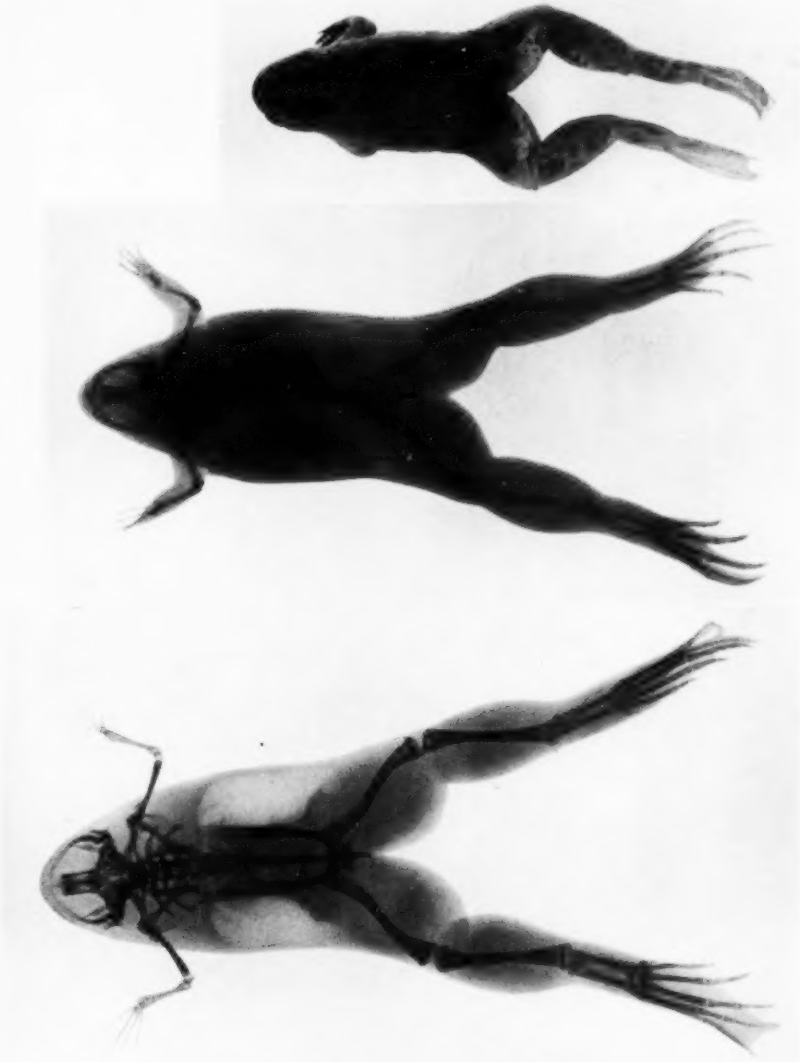
EXPLANATION OF PLATE.

Xenopus gilli sp. nov.

1. Ventral view of female.
3. X-ray of female.
4. Dorsal view of adult male.

Xenopus laevis Daud.

2. X-ray of sub-adult specimen.



1 2 3 4

XENOPUS GILLI (1, 3, AND 4); XENOPUS LAEVIS (2).

Neill & Co., Ltd.

DESCRIPTIONS OF THREE NEW SPECIES OF ANOPLURA FROM SOUTH AFRICAN MAMMALS.

By G. A. H. Bedford, F.E.S.,
Research Officer, Division of Veterinary Education and Research, Onderstepoort.

(With six Text-figures.)

Linognathus taurotragus nov. sp.

Male.—*Head* conical; on the dorsum of the pre-antennal area there is a row of four short hairs behind the oral region, a short one on each side in front, a longer one on the margin between the mouth and antenna, and another below this. Between the antennae there are two hairs on each side and a longer one below these. On the post-antennal area there are four hairs on the dorsum on each side of the meson, the last pair being close together, one nearer the temporal margin and another above it on the margin. On the venter there are two hairs on each side of the meson in front of the antennae and a long admedian pair behind the antennae.

Thorax with two short hairs at each latero-anterior angle and one a short distance from these on the inner margin. Between this one and the spiracle there is a longish hair, and below this one and nearer the middle there is a short and a long hair.

Abdomen brown, with pale lines between the segments in mounted specimens. On the dorsum of the first segment there is a longish hair and several short ones on each side of the meson; second to fifth tergites each with one long and two short hairs on each side of the meson; sixth and seventh tergites each with a row of four hairs; eighth tergite with a row of about ten hairs; apical segment with a row of about eight fine hairs on each side of the meson, and two long and several short ones on the margin. Spiracular hairs on the fourth and fifth segments short, long on the sixth and eighth segments. On the venter there are two or three hairs in the middle of each of the first three segments; fourth to seventh sternites with a row of about ten to twelve hairs, and a median row of about five to six hairs above; eighth sternite with two long admedian hairs and one or two short ones between these and the lateral margin.

Female.—Head and thorax as in the male, but the chaetotaxy of the abdomen is somewhat different. First tergite with two irregular rows of six to eight hairs, the admedian ones being longer than the others; second

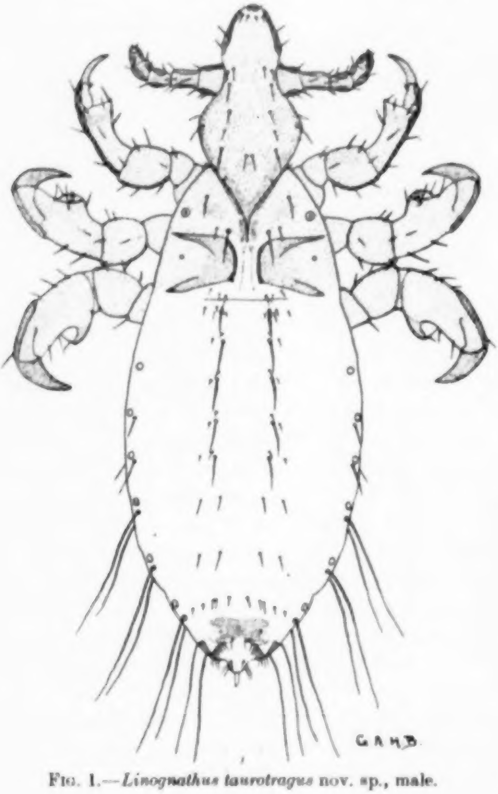


Fig. 1.—*Linognathus taurotragus* nov. sp., male.

Fig. 2.—*Linognathus taurotragus* nov. sp.; gonopods and genital mark of female.

to sixth tergites each with a row of four hairs, the inner ones being longer than the outer hairs; in addition, the fourth tergite has three hairs in the middle above these, and the fifth two; seventh and eighth tergites each with a row of six hairs; apical tergite with a transverse dark band, and a row of four hairs on each side below the band near the lateral margin and one in the band above these. Gonopods and genital mark as shown in fig. 2. On each side of the gonopods there are three to four hairs, and

above the genital mark an irregular patch of about nine short hairs. Apical sternite with a chitinized plate on each side; on the posterior margin of each plate there are about eight long hairs; between each plate and the gonopods there is a fringe of long hairs and about eight minute hairs in the middle of the sternite.

Measurements.

	Male.		Female.	
	Length.	Width.	Length.	Width.
Head . . .	0·61	0·31	0·66	0·35
Thorax . .	0·36	0·56	0·37	0·6
Abdomen . .	1·2	0·73	1·65	0·95
Total . .	2 mm.		2·53 mm.	

Described from several males and females taken off a *Taurotragus oryx* (eland) at Clocolan, O.F.S., in August 1920.

Cummings, who has given a figure of the male genitalia (Proc. Zool. Soc. Lond., p. 266, March 1916), regarded this species as a variety of *L. tibialis* Piaget, but I consider it more closely allied to *L. vituli* than to *L. tibialis*. Should Cummings prove to be correct, then Waterston's *var. euchore*, found on the springbok, is certainly not a variety of *L. tibialis*. The gonopods of the female of *L. taurotragus* resemble those of *L. vituli*, and the male genitalia are somewhat similar, but it can easily be distinguished from *L. vituli*, *inter alia*, by its large size and the pre-antennal area of the head being broader.

Linognathus gnu nov. sp.

Female.—*Head* widest at the temples; pre-antennal area long, with a short hair on each side near the oral region, and two short ones between them on the dorsum; a short distance behind these there is a transverse row of four short hairs, and on the margin in front of the antennae there are two hairs, one above the other. Between the antennae there are two short hairs on each side. On the post-antennal area there are two hairs on each temporal margin, and six long hairs on the dorsum on each side of the meson, the first and fifth pairs being the longest and the last pair nearest the middle. On the venter there is a transverse row of four hairs a short distance in front of the antennae, and two admedian longish hairs behind the antennae.

Thorax with a long hair on each side above the spiracle, and one or two minute hairs and two long ones on the inner side of each spiracle.

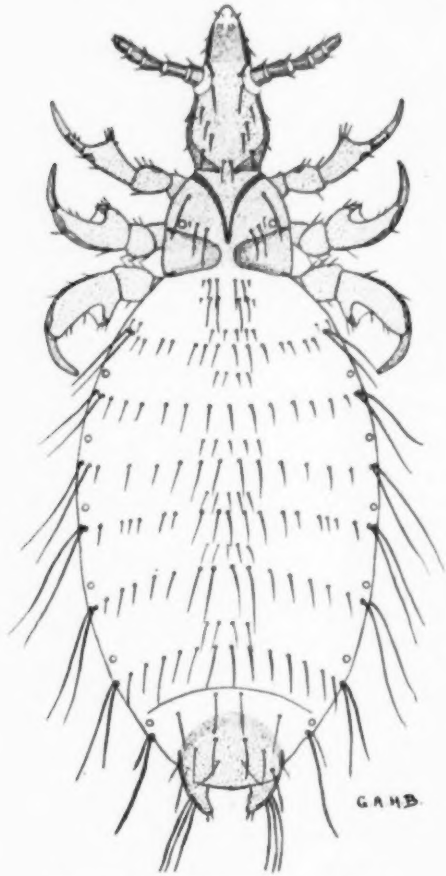


FIG. 3.—*Linognathus gnu* nov. sp., female.

FIG. 4.—*Linognathus gnu* nov. sp.; ventral surface of terminal abdominal segments of female.

Abdomen elongated-oval; segmentation indistinct, except between the seventh and eighth segments. On the dorsum there are two rows of six hairs on the first segment; second to seventh segments each with a transverse row of thirteen to seventeen hairs, and a short median row of four to five hairs above. Eighth segment with a row of four hairs; apical

segment with a dark transverse band and eight hairs. Second to eighth segments with long hairs on the lateral margins. Chaetotaxy of the venter similar to that on the dorsum. The hairs of the first row are not so numerous; there is a patch of short hairs above the genital blotch and about ten hairs between the gonopods. Gonopods with about eleven hairs.

Measurements.

Female.	Length.	Width.
Head . . .	0·75	0·3
Thorax . . .	0·43	0·43
Abdomen . .	1·8	1·06

Described from two females taken off a *Connochaetes gnu* Zimm. (black wildebeest), at Clocolan, O.F.S., by the writer on the 18th August 1920.

Linognathus ferrisi nov. sp.

MALE.—*Head* with the pre-antennal area pointed in front, rounded at the sides; on each side of the oral region in front there is a short hair and two short ones on each lateral margin. On the dorsum there are two hairs on each side of the meson between the antennae, one above the other, and five more admedian hairs below these, the last pair being close together, and one on each temporal margin. On the venter there are two short hairs on each side of the meson in front of the antennae, and a longish admedian pair below the antennae.

Thorax with a longish hair on each side between the latero-anterior angle and the spiracle, and two short and one long hair on the inner side of each spiracle.

Abdomen without distinct segmentation. The first two tergites each with a row of four short hairs in the middle, and on the lateral margin of the second there are about five short hairs. Third to sixth tergites each with two rows of hairs, the first row consisting of four to eight hairs and the second twelve to sixteen. Seventh tergite with a row of short hairs and two widely separated hairs above. Eighth tergite with two admedian hairs. Apical segment bare, except for a short hair on each lateral margin. Spiracular hairs long. Chaetotaxy of the sternites similar to that on the tergites, except that the hairs are not so numerous, especially on the sixth and seventh sternites, and for the most part slightly longer and stronger than on the dorsum. Genitalia as shown in fig. 6.

Measurements.

	Length.	Width.
Head . . .	0·53	0·23
Thorax . . .	0·31	0·36
Abdomen . .	1	0·61

Described from a single male collected by the writer off *Gorgon taurinus*

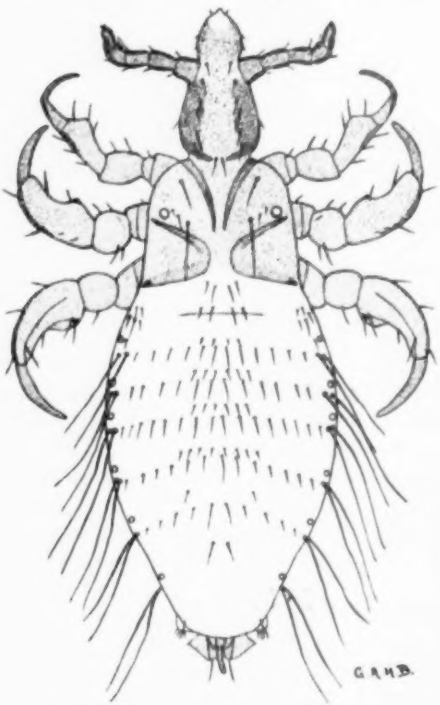


FIG. 5.—*Linognathus ferrisi* nov. sp., male.

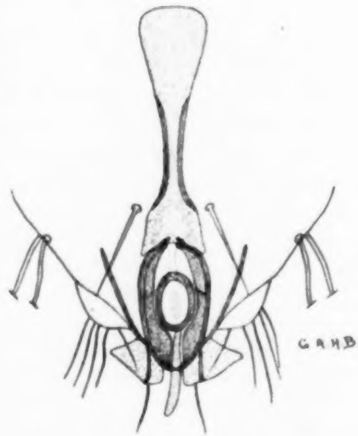


FIG. 6.—*Linognathus ferrisi* nov sp., male genitalia.

Burch. (blue wildebeest), in the Zoutpansberg district, northern Transvaal, on the 26th July 1924.

I have much pleasure in naming this species after Professor G. F. Ferris of the Stanford University, California, whose works on the Anoplura are well known.

THE CHEMISTRY OF THE ROOT OF *XYSMALOBIUM UNDULATUM*, R.Br.

(South African National Herbarium No. 3299.)

By Maria G. Brandwijk.

(From the Pharmacological Laboratory, University of the Witwatersrand, Johannesburg.)

1. Introduction.

The attention of Professor J. M. Watt was first drawn to this plant and its medicinal uses by the late Mr. T. I. Norton of Elsburg, Transvaal. He stated that a tincture or infusion of the dried root is used in dysenteries and diarrhoeas, for dyspepsia and indigestion, and as a " uterine sedative."

Mr. Norton supplied this laboratory with a large stock of the dried roots and with specimens of the plant. The latter were submitted to the Division of Botany of the Department of Agriculture, Union of South Africa, which determined the plant as *Xysmalobium undulatum*, R.Br., family—Asclepiadaceae. These specimens (Watt and Brandwijk No. 8 *) have been housed in the South African National Herbarium under No. 3299.

The plant has been known to popular medicine in South Africa for many years under various botanical names. Thunberg,[1] Smith,[2] and Marloth [3] have all mentioned its use as a medicine. The common names are " Chonga," " Ishongwe," and " Bitter-wortel."

2. Method of Extraction.

I set out with the idea of isolating, if possible, the active principle or principles, and incidentally to note any other facts regarding the chemistry of the root which might emerge.

In order to find out which was the best extracting medium for obtaining the toxic principle or principles, six small percolators were put up as follows :—

In each was placed 25 grm. of powdered root (No. 60 powder). The

* Serial No. of plant in Collection of South African Medicinal and Poisonous Plants made by Watt and Brandwijk.

material was macerated for twenty-four hours, and then percolated until the percolate came through colourless, with the following media :—

No. 1. Absolute alcohol.
,, 2. Alcohol 90 per cent.
,, 3. Distilled water.
,, 4. Chloroform.
,, 5. Alcohol 70 per cent.
,, 6. ,, 45 ,,

In Nos. 3, 5, and 6 the percolate was of a dark-brown colour, in No. 2 yellow, in No. 1 a lighter yellow, and in No. 4 practically colourless. These percolates were evaporated down on the water-bath and the residues taken up in distilled water.

On injecting into frogs, there seemed little difference in the relative toxicity of Nos. 1, 2, 3, 5, and 6. No. 4 produced practically no effect ; 45 per cent. alcohol was therefore chosen as the extracting medium, for cheapness and also in order to avoid fermentation.

Three kilos of dried root in No. 60 powder was macerated for twenty-four hours with sufficient 45 per cent. alcohol, and was then carefully and evenly packed into percolators. The percolators were allowed to stand for twenty-four hours with about ½ inch of fluid on top of the powder. Percolation was then commenced and continued at a slow and steady rate until the fluid came through colourless. This took about two and a half months, and so in the meanwhile the following work was done on the dried powdered root itself.

3. Water, Ash, etc., of the Root.

Water.—When the powder was dried in an oven at 105° C. there occurred an average loss of water of 10·3 per cent.

Ash.—The average ash is 4·9 per cent.

The average percentage of *constituents soluble in rectified spirit* is 20·3.

Starch, Dextrin, and Sugar.—The total carbohydrates, after hydrolysis, was first estimated and an average of 35·4 per cent. was found, expressed as glucose. The average percentage of free sugar, estimated before hydrolysis and expressed as glucose, was found to be 7·6. It will thus be seen that the carbohydrates minus free sugar is 27·8 per cent. expressed as glucose, and 25 per cent. expressed as starch ($27{\cdot}9 \times 0{\cdot}9 = 25$).

4. Steam Distillation.

In order to see whether the aromatic odour of the root was due to the presence of a volatile oil, 30 grm. of the powdered root was mixed with

acidified water (phosphoric acid) and subjected to steam distillation. The distillate was slightly turbid, had a mawkish odour and contained no volatile oil. When the fluid was evaporated off, there was left a mere trace of residue. The distillate was neutral to both litmus and methyl orange and therefore did not appear to contain any volatile organic acid. It was injected into a cat and produced no effects.

After this acid distillation, the mixture of powdered root and acidified water was made alkaline with sodium carbonate and again subjected to steam distillation. The distillate was again slightly turbid, yellowish in colour, had a mawkish odour and was alkaline to litmus and phenolphthalein. No volatile alkaloids could be identified. A very slight residue was left on evaporating down. The distillate injected into a cat produced no effects.

From this it will be seen that the root contains no volatile active substances.

5. The Percolate.

The percolate was acid to litmus and, in case the active principle or principles were glucosidal in character, the percolate was made alkaline by the addition of sodium carbonate before proceeding to evaporate off the alcohol. The alcohol was evaporated off and the residue evaporated down on the water-bath in an open dish until the extract was dry when cold. From the 3 kilos of root 924 grm. of dry extract was obtained. When exposed to the atmosphere, it was found to take up water readily and became first sticky and later fluid. For storage, the extract was reduced to a fine powder in a mortar and kept over calcium chloride.

This extract was found to be very toxic to frogs, rabbits, cats, and dogs.

6. The Extract.

Tannic Acid.—As it was stated that the root acted as an anti-diarrhoeic agent, the extract was tested for tannic acid. All these tests were negative and the extract does not contain tannic acid.

Gum.—The extract contains gum in large quantities. In order to separate the gum from the other constituents, the following two methods were tried :

A.—19 grm. of extract was suspended in a small quantity of water (about 25 c.c.). This suspension was treated with absolute alcohol, which produced a brown precipitate. The precipitate was filtered off and the filtrate evaporated down until it was of a syrupy consistence. Absolute alcohol was again added, with the production once more of a brown precipitate. This was filtered off. The filtrate was again treated in the

same way, when practically no precipitate was obtained by the addition of the alcohol.

The precipitates were collected and mixed and dried on the water-bath. The result was a dark brown mass. Apparently part at least of the colouring matter was precipitated. After weighing, it appeared that the extract contained about 61 per cent. of gums.

The filtrate was evaporated down, resulting in a dark brown mass. It gave a strongly positive reaction with aniline acetate and hydrochloric acid, showing that the gums had not been fully precipitated by the absolute alcohol.

The precipitate and the filtrate were both tested on animals. Both were found to be markedly toxic, though the precipitate appeared to be somewhat less toxic than the filtrate. The difference in the degree of toxicity was not marked.

It is thus seen that this method is unsatisfactory for isolating the toxic principles in a more or less quantitative way because

(*a*) the gums are not fully precipitated ;
(*b*) the toxic portion appears to distribute itself more or less equally between precipitate and filtrate.

B.—A quantity of the extract was subjected to extraction with different solvents, using the one after the other on the same portion of extract.

(1) Extracted in a soxhlet apparatus with dry ether for about six hours. The ether was evaporated off, leaving a trace of residue.
(2) The remainder was then exhausted with dehydrated alcohol on a water-bath and the alcohol filtered off. This procedure was repeated several times, until the filtrate, which at first was brown, came off nearly colourless. The filtrates were then mixed and the alcohol driven off. The residue was dark brown in colour and was weighed. It represented about 46 per cent. of the extract.
(3) The remainder of the extract left after the alcoholic extraction was soluble in cold water. When dry, it represented about 50 per cent. of the extract.

Both the products obtained under (2) and (3) gave a strong gum reaction.

All three products were tested on animals with the following results : (1) was practically non-toxic, (2) and (3) were about equally toxic. This method appeared also therefore to be unsuitable for the separation of gums and active principles.

Some general reactions were done on the different separation products.

(1) was colourless and insoluble in water ; faintly acid to litmus. Tests for organic acids were negative ; did not reduce Fehling's solution, either

before or after boiling with acid. Alkaloidal reactions all negative. It seems therefore that this fraction contains no organic acids, no carbohydrates or glucosides, and no alkaloids.

(2) was brown in colour and not wholly soluble in water, the solution having a slight suspension of undissolved material in it. Weakly acid to litmus. A micro-crystalline precipitate was obtained by acidifying this suspension and filtering, and adding to the filtrate liquor calcis. The suspension contains free and combined carbohydrate when tested with Fehling's solution. The suspension gives a positive reaction to different alkaloidal reagents. From these observations it appeared that product (2) may contain organic acids, carbohydrates and glucosides, and alkaloids.

(3) was brown in colour and soluble in water: weakly acid to litmus. Contains free and combined carbohydrates. Gives a positive reaction with alkaloidal reagents. The conclusion is that product (3) may contain carbohydrates, glucosides, and alkaloids.

Alkaloids.—The question of the possible presence of alkaloids was carefully explored. (3) was treated according to the method of Stas-Otto. In both the acid and alkaline ether extractions, a very slight residue was left. The residues gave no precipitate whatever with the alkaloidal reagents. The same results were obtained using product (2). It may therefore fairly be concluded that the extract does not contain any alkaloids, but the alkaloidal reactions given by products (2) and (3) are due to precipitation by some other principle.

Glucosides.—The possible presence of glucosides was then investigated. It is known that tannic acid is often used for the precipitation of glucosides.(4) A small quantity of the extract was suspended in a very small quantity of water, and ammonia added until the suspension was just alkaline. To this was added a 20 per cent. solution of tannic acid, when a precipitate appeared which was brown in colour. Care had to be taken not to use an excess of tannic acid, because this seemed to redissolve the precipitate. The precipitate was filtered off and washed with water until the wash-water came off practically colourless.

The precipitate was dissolved in alcohol and marked (x). The first filtrate was kept and marked (y). These were tested on animals, and (x) was found to be very toxic while (y) was practically non-toxic. It appeared thus that tannic acid precipitated the toxic principle or principles almost completely.

A large quantity of the extract was now taken and treated in the same way. The precipitate was well washed and then mixed with water and zinc oxide. This mixture was dried on the water-bath. When dry, it was powdered and extracted several times with rectified spirit in an erlenmeyer flask, using air condensation. From the extract the alcohol was distilled

off, and the residue dried in a desiccator over sulphuric acid. A dirty yellow crystalline product was thus obtained. The amount of this represented about 18 per cent. of the dry extract and 5·5 per cent. of the root.

This principle dissolves with difficulty in cold water, but readily in boiling water. It is also soluble in acids and alkalis. It dissolves with some difficulty in cold alcohol, easily in hot alcohol. The solution in water is neutral to litmus. Under the microscope the appearance is a mixture of crystalline and amorphous structure, the substance being evidently impure. It gives a positive reaction with the alkaloidal reagents, but contains no nitrogen. (This explains the positive alkaloidal reactions obtained previously.)

A solution in water of this impure product does not reduce Fehling's solution. If boiled with 2 per cent. sulphuric acid, it gives a slight reduction. After prolonged boiling with acid, the degree of reduction is much greater. It seems therefore that the product contains carbohydrates or glucosides which hydrolyse only after prolonged boiling with 2 per cent. sulphuric acid. When carrying out these procedures, it was found that the product first dissolved in the sulphuric-acid solution and then later, after a little time, there appeared a precipitate of the hydrolyte which was yellow in colour.

This impure product gives a positive reaction to tests for gums.

It was tested on animals and was found to have a toxic effect about three times as great as that of the dry extract.

Several methods of purification were tried. For example, the usual method of precipitation by ether from an alcoholic solution was first applied. The product thus obtained was amorphous and also contained gum, which could not be got rid of. The following method was then tried with much better results. The product dissolves with difficulty in cold water. Therefore, to get rid of the gum, a quantity was left with water for about twenty-four hours, stirring occasionally. The gum and colouring matter dissolved, the fluid becoming yellow in colour. The water was poured off and fresh water applied. After twelve hours this was filtered off. The remainder on the filter-paper dissolves with difficulty in cold, but easily in hot, alcohol and water. It was recrystallised first from hot 50 per cent. alcohol and then from boiling water. The fluids being still yellow in colour, these procedures were repeated and the fluids were then found to be colourless. The resulting product was pure white.

This white product appeared crystalline under the microscope, and showed needles and bundles of feathers. At 175–177° C. the crystals shrink together, and at 177–179° C. they melt, decomposing at the same time with the formation of a brown fluid. This brown fluid solidifies on further heating.

In order to see whether a still purer product could be obtained, samples

were recrystallised from hot 50 per cent. alcohol, from boiling water, and by precipitation with ether from an alcoholic solution. The melting-points of the three products obtained in this way were the same as that which was previously got. The recrystallisation from boiling water gave a crystalline substance with the same appearance under the microscope. The other two products were amorphous. It is thus evident that the substance can be obtained in a pure state by the method just described, and that it can be obtained in a crystalline form only from boiling water. This substance I have named Xysmalobinum (Xysmalobine).

Xysmalobinum.

The amount obtained is about 1 per cent. of the extract, viz., about 0·3 per cent. of the dried root.

The substance dissolves with difficulty in cold water and alcohol, but easily in hot. It is practically insoluble in ether, chloroform, and amyl alcohol. It is tasteless.

Colour Reactions.—Concentrated sulphuric acid gives first brown red gradually changing into red, then the edges change to a blue colour, and after half an hour the whole of the fluid is deep blue, which colour becomes lighter and lighter until ultimately it disappears altogether. Fröhde gives first red brown, later red, and becomes after a quarter of an hour green.

It is precipitated by tannic acid and by a solution of iodine in potassium iodide, but not by the other alkaloidal precipitants. The precipitate with tannic acid dissolves in an excess of tannic acid.

Combustion and water estimation of the air-dried crystals gives an average of $C_{46}H_{70}O_{20}$, $5H_2O$.

Limited investigation of the structure was made, but without results.

It is much less toxic than the extract but, however, has some of the effects upon animals of the latter.

Hydrolysis.—Xysmalobinum, when heated with 2 per cent. sulphuric acid, dissolves, and after a time a yellow precipitate appears. This precipitate changes to an orange-red colour if it is left for a long time in contact with the acid. In the fluid, glucose was identified, but no other sugar was found. It requires prolonged boiling with 2 per cent. sulphuric acid to completely hydrolyse the glucoside. The best method appears to be to leave the glucoside in the acid in a boiling water-bath for about an hour. One molecule of the glucoside gives one molecule of glucose.

Hydrolyte.—The hydrolyte is yellow in colour, insoluble in water and acids, soluble with difficulty in cold alcohol, but more easily in hot. It is practically insoluble in ether. Under the microscope it is yellow in colour and amorphous. It decomposes at about 190° C. without having melted.

Reactions for group radicals were done without result. The hydrolyte was not tested on animals.

I conclude therefore that one of the active principles, though not the main *toxic* principle, is this glucoside which produces on hydrolysis a yellow amorphous insoluble hydrolyte.

Glucosides (continued).—The crude crystalline product, obtained after precipitation with tannic acid, drying the precipitate with zinc oxide and extraction with alcohol (see p. 357) was much more toxic than the extract. Xysmalobinum, on the other hand, was much less toxic than the extract. It seemed probable, therefore, that the main toxic principle had remained in solution in one of the fluids used during the purification. The only fluids used were 50 per cent. alcohol and water. The amounts used in washing and recrystallisation had fortunately been kept and were evaporated down to dryness on the water-bath, the alcohol and the water-soluble substances being kept separate.

The residues from recrystallisation from alcohol 50 per cent. (1) and from the wash-water together with those from the recrystallisation from water (2) were finely powdered. Both powders were slightly yellowish in colour, and were tested on cats. Both residues, given in doses of 10 mg. per kilo, proved toxic, producing vomiting and convulsions, and ultimately death. (2) was much more rapid in its action and appeared the more toxic material.

Attempts were then made to isolate a pure principle from (2). This slightly yellow powder is amorphous and contains a fair amount of gum. Two methods were used to try and get rid of this.

(*a*) Residue (2) was dissolved in absolute alcohol on a water-bath. The solution is yellowish and cloudy. After filtering, ether was added to the filtrate, which caused the separation of a pure-white precipitate. The fluid was sucked off and the precipitate washed with ether. The precipitate, as soon as the ether evaporates, deliquesces and becomes a yellowish sticky substance which forms a film over the filter paper. Some of this film was dissolved in water, which produced a very pale yellow solution. This solution proved very toxic to cats.

(*b*) As it was known that gums are often precipitated with lead-acetate or lead-subacetate, (2) was heated with water, resulting in an almost clear solution of a yellow colour. To this were added a few drops of lead-acetate solution. No precipitate was produced. Then solution of lead-subacetate was added, which produced a thick yellowish precipitate. This was filtered off, and the excess of lead in the filtrate was precipitated with hydrogen-sulphide solution. This was filtered off, and the filtrate evaporated down until the bulk was very small. In this way, the greater part of the acid was got rid of. A portion of the resulting fluid was neutralised with

sodium carbonate, giving a colourless solution. This was injected into a cat which died.

The rest of the solution was now evaporated down on the water-bath and a brown residue was left, having the appearance of a thick extract. This was dissolved in absolute alcohol and ether added. The result was a precipitate which behaved in the same way as the precipitate obtained with ether in (*a*). The amount of this precipitate was so small that it was impossible to work further with it.

Attempts were then made to obtain the precipitate in a more stable form by method (*a*). Part of (2) was dissolved in water, in which it dissolves very easily, even in cold water. With the addition of ether no precipitate was obtained. The substance is evidently not precipitated from a watery solution. It was therefore again precipitated with ether from a solution in absolute alcohol. The precipitate, this time, was of a very pale yellow colour and did not deliquesce when exposed to the air. Under the microscope it is amorphous. When heated, it melts.

This precipitate was once more dissolved in absolute alcohol and treated in the same way with ether. Unfortunately, only a very small amount was obtained in the amorphous state, the remainder deliquescing when exposed to the air and changing to a yellowish sticky film over the filter paper. This may perhaps be explained by assuming that in the second precipitation there were accidentally used the correct proportions of absolute alcohol and ether.

Glucosidal Product No. 2.

The precipitate is free from gums, by the phloroglucine-hydrochloride test. The solution in water is faintly yellow in colour and is neutral to litmus. It gives a very slight reduction of Fehling's solution. After hydrolysis the reduction becomes very marked. The substance appears, therefore, to be glucosidal also. During hydrolysis a hydrolyte is formed which dissolves when the solution is boiling and precipitates out on cooling.

This glucoside is very easily soluble in water and alcohol, insoluble in ether.

Colour Reactions.—With concentrated sulphuric acid there appears immediately a red-brown colour, changing to red and later becoming green from the edges. In half an hour the whole fluid is green. Fröhde produces first a chocolate-brown colour, which changes to deep red. In half an hour the edges are dirty green, and later the whole fluid becomes of the same colour.

With *tannic acid* a watery solution gives a thick precipitate which is amorphous and which dissolves in a large excess of tannic acid. *Iodine in*

potassium-iodide solution also gives a precipitate. Tests with other alkaloidal precipitants are negative. The substance has a slightly bitter taste.

7. Saponins.

It was observed that the extract, when it was shaken with water, frothed very readily. The extract also gives the colour reactions of the saponins, viz., with concentrated sulphuric acid it changes to yellowish red, later brown red, then deep red, and finally dark violet. This colour-change goes very rapidly.

A suspension of defibrinated blood 1 : 100 in physiological salt solution was made. If extract is added to this, the blood is lysed in half a minute.

To a watery suspension of the extract, lead-acetate was added in order to precipitate any acid saponins which might be present. A thick precipitate appeared. This was filtered off and, after washing, the lead was precipitated with hydrogen-sulphide solution. The solution was then filtered again and the filtrate evaporated down to a small bulk. This fluid was salted out with ammonium sulphate, when a precipitate appeared which was shaken out with amyl alcohol. On evaporating off the amyl alcohol, there remained a dry residue which was numbered (1).

The filtrate from the lead-acetate precipitation was treated with a solution of lead-subacetate in exactly the same way, with a view to precipitating any neutral saponins which might be present. A thick precipitate resulted which was treated in the same way. Finally a dry residue was obtained which was numbered (2).

Solutions were made of (1) and (2) in physiological salt solution. To these was added a suspension of defibrinated blood 1 : 100 in physiological salt solution. (1) showed haemolysis in about two minutes with a very concentrated solution. (2) gave no haemolysis. Neither ammonium sulphate nor amyl alcohol produce haemolysis. Both (1) and (2) produce discoloration of the blood in saline, the colour changing from red to a dirty yellow. Neither ammonium sulphate nor amyl alcohol causes discoloration.

With concentrated sulphuric acid, (1) gives a yellowish-red colour, which later changes to brown red, and finally to reddish violet: (2) gives a yellowish-red colour, changing to brown red, then to red, lastly to green. The acid which was used was tested with saponin and gave a yellowish-red colour, changing to red, and later to red violet. Fröhde produces with (1) a red-brown colour, which becomes red and later green from the edges; with (2) a brown colour, changing to red brown, red, and finally edges green. Saponin gave after quarter of an hour blue violet, changing after a further quarter of an hour to a rather clear green.

The conclusion, therefore, is that saponins seem to be present, but in very small quantity and of the less toxic kind, viz. acid. There seems to be present also a principle which produces a discoloration of blood.

The latter effect was investigated further. The stock solution used was a 1 per cent. suspension of defibrinated blood in 0·9 per cent. saline.

(*a*) On adding solution of the *extract*, the blood suspension becomes clear and loses its red colour. The fluid becomes brownish, probably mainly from the extract. On spectroscopic examination, the usual broad absorption-band of oxy-haemoglobin near the D line is still present. The whole spectrum is very dark, and towards the violet end neither colours nor absorption-bands could be made out. There were no bands in the red.

(*b*) On adding solution of *acid-saponins* from extract, there occurred lysis and change in colour from red to dirty yellow. The spectrum was that of oxy-haemoglobin.

(*c*) Solution of *neutral-saponins* from extract does not produce lysis, but the colour change from red to dirty yellow is seen. The spectrum is that of oxy-haemoglobin.

The solutions and salts used in separating out the above saponins were also tested, and produced neither lysis nor colour-change. The various glucosidal products were also tested and found to give negative results.

The lysing action of the small quantity of saponins which appear to be present in the extract is not apparent during the experimental injection of the material intravenously. The colour change which has just been described is very definite, but I cannot explain it.

8. Preparation of a Glucoside from the Root Direct.

Three hundred grm. of the powdered root (No. 60 powder) was extracted on the water-bath with methyl alcohol in an erlenmeyer flask for about an hour, using an air condenser. The alcohol was filtered off. The procedure was repeated with the same sample of root. The two filtrates were mixed and the methyl alcohol evaporated off. The residue was dissolved in boiling water and filtered. In the filtrate there appeared a precipitate on cooling. This precipitate was recrystallised from methyl alcohol and then was greyish white in colour. It was washed with ether but remained greyish white. It was thereupon recrystallised from boiling water, when a white precipitate was obtained. The amount represented about 0·1 per cent. of the dried root.

This product is a glucoside, the sugar being glucose. Microscopically it

consists of soft needles. The following is a comparison of this glucoside with Xysmalobinum.

Test.	Xysmalobinum.	Glucoside direct from Root.
Sugar . . .	Glucose	Glucose
Colour . . .	White	White
Solubility :		
Water . . .	Soluble	Soluble
Alkali . . .	,,	,,
Acid . . .	,,	,,
Ether . . .	Insoluble	Insoluble
Hot alcohol . .	Soluble	Soluble
Microscopically . .	Needles and feathers	Needles
Colour reactions :		
Concentrated H_2SO_4	Brownish, later blue	Brownish, later blue
Fröhde . . .	,, ,, green	,, ,, green
Precipitation reactions :		
I_2 in KI . .	Precipitate	Precipitate
Tannic acid . .	Precipitate soluble in excess	Precipitate soluble in excess
Other alkaloidal precipitants . .	No precipitate	No precipitate
Melting-point .	176° C. shrinks together 177–179° C. melts	183° C. shrinks together 187° C. melts
Taste . . .	None	None
Percentage in root .	0·3 per cent.	0·1 per cent.
Action on cat . .	50 mg. per kilo does not kill, but cat very ill.	50 mg. per kilo kills after some delay. Symptoms while under observation not severe.
	Produces a marked rise in blood-pressure and diuresis.	Produces marked fall in blood-pressure and inhibition of the urinary secretion.

Though it would appear, from a superficial examination of the foregoing comparison, that these two glucosides, viz., Xysmalobinum and the glucoside prepared direct from root, resemble each other very closely, there are several definite differences. The melting-points are not the same, the appearance under the microscope differs slightly, and they differ in toxicity and action on animals. Though the work on animals is insufficient to make a definite conclusion possible, it appears that these two glucosides are probably *not* identical.

9. Conclusions.

1. I have isolated from the dry extract of the root:

   (*a*) an apparently pure glucoside which I have named Xysmalobinum. This does not appear to be the main toxic principle;

   (*b*) another glucosidal product which deliquesces very readily and is thus very difficult to handle. The main toxic principle appears to be contained in this product.

2. I have also isolated direct from the root an apparently pure glucoside. Chemically, this somewhat resembles Xysmalobinum, but the two do not appear to be identical. The toxicity is low compared with that of the extract.

3. The extract contains a very small amount of acid-saponins and a substance which changes the colour of blood from red to a dirty yellow (using 1 per cent. suspension of blood).

4. The extract does not contain any volatile active products, any alkaloids, or any tannic acid.

5. The extract contains a large proportion of gum.

10. Acknowledgments.

I have to thank the Division of Botany for determining the plant and for their interest in this investigation. Thanks are also due to the late Mr. T. I. Norton for supplying the root with which this work was carried out, and to Messrs. B. Owen Jones, Wholesale Pharmacists, for powdering the root.

I am indebted to Professor J. M. Watt, Director of this Laboratory, for testing the toxicity of the various products which were isolated, and for the interest which he has shown in this investigation.

The bulk of the expenses have been defrayed by a grant from the Research Grant Board, Union of South Africa.

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THE THEORY OF HESSIANS FROM 1883 TO 1914.

By Sir Thomas Muir, F.R.S.

The interest taken in the theory of Hessians during this comparatively recent period is not appreciably greater than during the period (1880–1894) immediately preceding. Neither on the algebraical nor on the geometrical side is there an increase of contributions. Probably this is in part due to the fact that at the outset the Hessian had for its basic function the Cartesian representative of a locus, and that thus, not unnaturally, a restriction to such functions came to be the rule—a restriction that was of course encouraged by the name Hessian being given in some quarters (Hist., ii, p. 393) to the locus itself. In the third paper herewith reported on there is at least a marked breaking-away from such a narrow usage.

Muir, T. (1883).

[Question 11814 or 14987. Educ. Times, xlvi, p. 37; liv, p. 465; lv, p. 336; lxi, p. 80: or Math. from Educ. Times, (2), viii, p. 48; (2), xiv, pp. 38–39.]

The result sought to be established here is that if

$$u=ax^3+3bxy^2+3cxy^2+dy^3+e=0,$$

then

$$\frac{\partial^2 y}{\partial x^2}\left(\frac{\partial u}{\partial x}\right)^3=2e\begin{vmatrix} a & b & c \\ b & c & d \\ y^2 & -xy & x^2 \end{vmatrix}.$$

The most helpful solution is that given by Nanson, who not only makes the desired extension to the case where the determinant involved is the Hessian of *any* binary quantic, but proceeds to further generalisation. The ungeneralised result originally appeared in November 1883 in an examination paper of Glasgow University.

Voss, A. (1886 $/_3$).

[Ueber eine Eigenschaft der cubischen Formen mit beliebig vielen Veränderlichen. Math. Annalen, xxvii, pp. 515–526.]

The property in question is a further generalisation of Hesse's theorem of 1844 (Hist., ii, p. 377) regarding the Hessian of the Hessian of a cubic,

the previous extension of it to four variables having been effected by G. Bauer in 1883 (Hist., iv, p. 353).

MUIR, T. (1901 /$_1$).

[The Hessian of a general determinant. Transac. R. Soc. Edinburgh, xl, pp. 203–207.]

There being n^2 independent variables in a general n-line determinant, the Hessian of the determinant with respect to the said variables must be a determinant with n^2 lines: and what is established here is the fact that this latter determinant contains as a factor the $n(n-2)^{th}$ power of the original. The essence of the procedure is the multiplying of the Hessian of the given determinant $|a_{1n}|$ by the n^{th} power of $|a_{1n}|$, then the transposition of the product into an arithmetical multiple of $|A_{1n}|^n$, and finally the removal from this of the introduced factor $|a_{1n}|^n$. For example, the given determinant being $|a_1b_2c_3|$, we have

$$H(|a_1b_2c_3|)\,.\,|a_1b_2c_3|^3$$

$$=\begin{vmatrix} \cdot & \cdot & \cdot & \cdot & c_3 & -c_2 & \cdot & -b_3 & b_2 \\ \cdot & \cdot & \cdot & -c_3 & \cdot & c_1 & b_3 & \cdot & -b_1 \\ \cdot & \cdot & \cdot & c_2 & -c_1 & \cdot & -b_2 & b_1 & \cdot \\ \cdot & -c_3 & c_2 & \cdot & \cdot & \cdot & \cdot & a_3 & -a_2 \\ c_3 & \cdot & -c_1 & \cdot & \cdot & \cdot & -a_3 & \cdot & a_1 \\ -c_2 & c_1 & \cdot & \cdot & \cdot & \cdot & a_2 & -a_1 & \cdot \\ \cdot & b_3 & -b_2 & \cdot & -a_3 & a_2 & \cdot & \cdot & \cdot \\ -b_3 & \cdot & b_1 & a_3 & \cdot & -a_1 & \cdot & \cdot & \cdot \\ b_2 & -b_1 & \cdot & -a_2 & a_1 & \cdot & \cdot & \cdot & \cdot \end{vmatrix} \cdot \begin{vmatrix} a_1 & a_2 & a_3 & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ b_1 & b_2 & b_3 & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ c_1 & c_2 & c_3 & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & a_1 & a_2 & a_3 & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & b_1 & b_2 & b_3 & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & c_1 & c_2 & c_3 & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & a_1 & a_2 & a_3 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & b_1 & b_2 & b_3 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & c_1 & c_2 & c_3 \end{vmatrix}$$

$$=\begin{vmatrix} \cdot & \cdot & \cdot & -B_1 & A_1 & \cdot & -C_1 & \cdot & A_1 \\ \cdot & \cdot & \cdot & -B_2 & A_2 & \cdot & -C_2 & \cdot & A_2 \\ \cdot & \cdot & \cdot & -B_3 & A_3 & \cdot & -C_3 & \cdot & A_3 \\ B_1 & -A_1 & \cdot & \cdot & \cdot & \cdot & \cdot & -C_1 & B_1 \\ B_2 & -A_2 & \cdot & \cdot & \cdot & \cdot & \cdot & -C_2 & B_2 \\ B_3 & -A_3 & \cdot & \cdot & \cdot & \cdot & \cdot & -C_3 & B_3 \\ C_1 & \cdot & -A_1 & \cdot & C_1 & -B_1 & \cdot & \cdot & \cdot \\ C_2 & \cdot & -A_2 & \cdot & C_2 & -B_2 & \cdot & \cdot & \cdot \\ C_3 & \cdot & -A_3 & \cdot & C_3 & -B_3 & \cdot & \cdot & \cdot \end{vmatrix} =(-)^3 2 \begin{vmatrix} A_1 & B_1 & C_1 & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ A_2 & B_2 & C_2 & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ A_3 & B_3 & C_3 & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ B_1 & \cdot & \cdot & A_1 & -B_1 & C_1 & \cdot & \cdot & \cdot \\ B_2 & \cdot & \cdot & A_2 & -B_2 & C_2 & \cdot & \cdot & \cdot \\ B_3 & \cdot & \cdot & A_3 & -B_3 & C_3 & \cdot & \cdot & \cdot \\ C_1 & \cdot & \cdot & \cdot & \cdot & \cdot & A_1 & B_1 & -C_1 \\ C_2 & \cdot & \cdot & \cdot & \cdot & \cdot & A_2 & B_2 & -C_2 \\ C_3 & \cdot & \cdot & \cdot & \cdot & \cdot & A_3 & B_3 & -C_3 \end{vmatrix}$$

$$=(-)^5 2\,|A_1B_2C_3|^3=-2\,|a_1b_2c_3|^6$$

and therefore finally

$$H(|a_1b_2c_3|)=-2\,|a_1b_2c_3|^3.$$

The case where n is 4 is dealt with in similar fashion, even greater detail being entered into so as to justify the drawing of the general conclusion

$$H(\,|\,a_{1n}\,|\,)=(-)^{\frac{1}{2}(n-1)(n-2)}\,.\,(n-1)\,.\,|\,a_{1n}\,|^{\,n(n-2)}.$$

PASCAL, E. (1902 $^{18}/_{12}$).

[A proposito di una recente ricerca del Dottor Muir sull' Hessiano di un determinante. Rendiconti . . . Ist. Lombardo . . . (2), xxxv, pp. 941–950.]

The contents of this paper may be briefly described as a re-exposition of Muir's theorem and mode of proof, accompanied by deductions and extensions. In the first place an independent existence, under the title Lemma I, is given to the latter portion of the said proof in which was discussed the peculiar determinant of order n^2 arising from multiplying the Hessian of $|\,a_{1n}\,|$ by $|\,a_{1n}\,|^{n}$. Thereupon is suggested a similar result of interest called Lemma II: also, a deduction of a different type: *If* $|\,a_{1n}\,|$ *have the characteristic* n$-$1, *its Hessian cannot have a characteristic lower than* n. Next, it being recalled that the Hessian of $|\,a_{1n}\,|$ is a determinant whose non-zero elements are secondary minors of $|\,a_{1n}\,|$, the suggestion arises as to the effect of replacing the said minors by the two-line minors; and, the determinant so formed being denoted by K, it is found that

$$K=(-1)^{\frac{1}{2}(n-1)(n-2)}\,.\,(n-1)\,.\,|\,a_{1n}\,|^{\,2n(n-2)},$$

the simple fact being that the one equality is the "complementary" (Hist., iv, pp. 6–8) of the other. Finally, a determinant of order n^3 is formed from K and shown to be equal to $(n-1)^{2n}\,|\,a_{1n}\,|^{\,nn}$.

NICOLETTI, O. (1903 $^{28}/_{2}$).

[Sull' Hessiano di un determinante. Rendiconti . . . Ist. Lombardo, (2), xxxvi, pp. 470–476.]

The subject continues the same, Nicoletti following up Pascal, as Pascal followed up Muir. The procedure, however, is entirely different, Muir's theorem, for example, being now sought to be established by a gradational mode of proof—that is to say, by basing the truth of any case on the truth of the case preceding. With this in view a number of auxiliary theorems are at the outset brought forward and discussed, the general subject of them being the effect which a change performed on a determinant entails upon the Hessian of the determinant. The most interesting of these, when n is 4, is *If in the Hessian of* $|\,a_1b_2c_3d_4\,|$ *we put* $d_4=1$, $d_3=d_2=d_1=0=c_4=b_4=a_4$, *thus reducing* $|\,a_1b_2c_3d_4\,|$ *to* $|\,a_1b_2c_3\,|$ *the result is* $\frac{3}{2}\,|\,a_1b_2c_3\,|^{5}\,.\,H(\,|\,a_1b_2c_3\,|\,)$.

Pascal's theorem regarding the characteristic of the Hessian is changed into *If the characteristic of an* n-*line determinant be* n−1, n−2, *or* <n−2, *the characteristic of its Hessian will be* 2n, 4, *or* 0 *respectively.* Pascal's determinant K is similarly discussed.

GRAVÉ, D. A. (1903).

[On certain properties of the Hessian (in Russian). Reports of the Phys.-Math. Soc. (Kieff), No. 6, pp. 1–9.]

The interest of this is mainly geometrical; but, so far as it does not directly concern the *locus* of the Hessian, it has a bearing in connection with Sylvester's theorem of 1879 regarding the roots (Hist., iii, p. 371).

MUIR, T. (1906 $^{7}/_{8}$).

[The Hessians of certain invariants of binary quantics. Proceed. R. Soc. Edinburgh, xxvi, pp. 529–532.]

The two results established here are (1) *The Hessian of the cubinvariant of a binary quantic is* 8 *times the product of the said invariant by the quadrinvariant*; (2) *The Hessian of the discriminant of the binary cubic is* $\frac{1}{3}$ *of the square of the said discriminant.* They are purely determinantal results, the fundamental step in the procedure—an indirect step or artifice—being the multiplication of the Hessian of the invariant by the invariant itself—that is to say, by the persymmetric determinant P(a, b, c, d, e) in the one case, and by the bigradient $\begin{vmatrix} (a,\ 2b,\ c)_2 \\ (b,\ 2c,\ d)_2 \end{vmatrix}$ in the other.

STEPHANOS, C. (1907 $/_{1}$).

[Démonstration et généralisation d'une propriété d'un déterminant symétrique du troisième ordre. L'Intermédiare des Math., xiv, pp. 11–12.]

The property in question appears here in the form of an evaluation of the Hessian of the discriminant of an n-ary quadric, the author appropriately pointing out its connection with the fact that the Hessian of an invariant is itself an invariant. He does not seem, however, to have observed that there is a different angle at which he might have viewed it, namely, as the Jacobian of the elements of the adjugate of an axisymmetric determinant D with respect to the elements of D: and that the desired result, in the slightly simpler form

$$J=(1-n)D^{\frac{1}{2}(n+1)(n-2)},$$

had thus been obtained in 1902 by a purely determinantal procedure. (See under date 1902 $^{18}/_{7}$ in chapter on Jacobians.)

MUIR, T. (1908 $/_2$).

[The theory of Hessians in the historical order of development up to 1860. Proceed. R. Soc. Edinburgh, xxviii, pp. 413–432.]

This, the first of our historical papers on Hessians, reports on nineteen (19) writings, beginning with Hesse's fundamental memoir of 1844 and including repeated communications by Cayley, Brioschi, and Sylvester, besides others by Hesse himself.

ROSS, C. M. (1910 $^1/_3$) : SWAMINARAYAN, J. C. (1912 $/_{12}$) : KREDIET, C. (1914).

[Question 16826. Educ. Times, lxiii, pp. 134, 208 : Math. from Educ. Times, (2), xviii, p. 82.]
[Question 433. Journ. Indian Math. Soc., iv, p. 239 ; v, pp. 149–151.]
[Jets over den determinant van Hesse. Wisk. Tijdschr., xi, pp. 228–232.]

The first result here is

$$H(x_1^2x_2^2\ \ldots\ x_n^2)=(-)^{n-1}2^n(2n-1)(x_1^2x_2^2\ \ldots\ x_n^2)^{n-1};$$

the second concerns the function

$$\begin{aligned}p_1(x_1+a_2x_2+\ \ldots\ +a_nx_n)^2+p_2&(x_2+b_3x_3+\ \ldots\ +b_nx_n)^2\\&+p_3(x_3+c_4x_4+\ \ldots\ +c_nx_n)^2\\&+\ \ldots\ldots\ldots\ldots\ +p_nx_n^2,\end{aligned}$$

the Hessian of which is shown to be $2^np_1p_2\ \ldots\ p_n$; in the case of the third the interest is purely geometrical.

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whose writings are herein dealt with.

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15*th March* 1927.

A METHOD FOR THE STUDY OF DISSOCIATION OF HAEMOCYANIN.

By Lancelot T. Hogben.

(With three Text-figures.)

The study of oxidation equilibrium in systems containing respiratory pigments has been the centre of considerable interest not only in physiology but in experimental medicine for the past two decades. Naturally the bulk of this work has been based on the haemoglobins, since the respiratory pigment of man's blood is a member of this family of proteins, but the demonstration of oxidation processes in the haemoglobins is, however important, a matter involving a technique so elaborate as to be beyond the range of laboratory accommodation for medical classes. There are nevertheless other reversibly oxidisible pigments which occur in the tissue fluids of animals in sufficient quantities for manipulations of this kind. Foremost of these come the family known as the haemocyanins. This term covers a group of respiratory proteins all characterised by the fact that the metallic constituent of the molecule is copper and that the change in colour on reduction is from an intense blue to a completely colourless solution. The reaction, like the reduction of oxyhaemoglobin, oxychlorocruorin (and the oxidised derivatives of other forms of respiratory protein such as helicorubin), is perfectly reversible: on being shaken vigorously *in vacuo* for a few seconds a deep blue solution of oxyhaemocyanin becomes quite colourless. On re-admitting air the solution regains its characteristic blue with equally dramatic rapidity. The nature of the colour change makes it possible to study oxidation equilibrium in the case of the haemocyanins with a simplicity of technique that is impossible in the case of the haemoglobins.

It is possible in the case of haemoglobin to estimate the degree of oxidation by a colorimetric procedure. Artificial standards ranging from the appropriate tint of scarlet to the appropriate extreme of purple can be manufactured, but their manufacture and calibration involves a previous determination of the colour of samples whose oxygen content has been determined by gas analysis, and their use implies the use of a standard concentration of respiratory pigment throughout. With haemocyanin this is not so. Since it is colourless when reduced, the addition of 10 c.c. water

(or water made slightly opalescent to match the reduced serum) to 90 c.c. of the fully oxidised serum will give a dilution identical in tint with serum 90 per cent. oxidised. Thus we can prepare in a few minutes a series of colour standards corresponding to different degrees of oxidation for any sample of blood that we are using. The advantage of this procedure does not only lie in providing a very rapid and direct method of estimating the degree of oxidation of the pigment, but also in getting rid of the need for

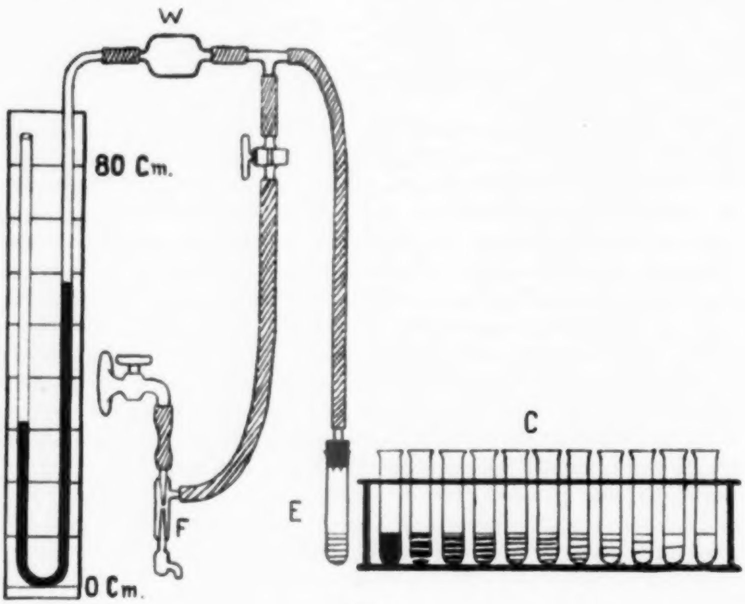

FIG. 1.

elaborate arrangements for submitting any given sample to gas mixtures of known concentration, when determining the variation of the equilibrium constant of the reaction for different conditions, such as temperature, hydrogen, on concentration and the like. Few physical experiences are more reliable than the oxygen content of the atmosphere. Thus, in order to study the relation between oxygen concentration and oxidation, one has merely to shake the sample in a tube connected with a manometer and pump at reduced pressure. On correcting for vapour pressure, as given in any physical tables, the oxygen partial pressure can be deduced at once by Henry's law. The concentration of oxygen in solution in the watery phase is a linear function of the partial pressure.

Some years ago, in seeking suitable materials for class-work in experimental zoology, the author found that oxyhaemocyanin can be reduced in a few minutes if shaken in a test-tube connected with a filter-pump. A crude method of colorimetric determination of the dissociation curve of haemocyanin suitable for students' use was described (Pantin and Hogben, 1925) for the benefit of teachers (fig. 1). Since that date the author has carried out researches (Hogben, 1925; Hogben and Pinhey, 1926; Hogben and Pinhey, 1927) which not only emphasise the general resemblance between the physical chemistry of the haemocyanins and haemoglobins but suggest new lines of inquiry in the latter field. In these researches more elaborate apparatus has been employed, permitting further reduction in time and effort and greater accuracy. The final details of these improvements have not as yet been placed on record. In view of the facts elicited, however, it seems desirable to place at the disposal of other teachers a method suitable to demonstrate analogous phenomena to those which occur in the oxidation and reduction of haemoglobin with a rapidity and simplicity of technique which renders it suitable to the short periods of time available for class-work.

2. Occurrence of Haemocyanin and Preparation of Blood.

The blue respiratory pigments known as the oxyhaemocyanins are usually said to occur in Molluscs and Arthropods. All that can be said with certainty, however, is that they occur in the following groups: in cephalopods, some gasteropods (snails, whelks), in decapod crustacea, and in some larger arachnids, notably Limulus. They are certainly not universally present in either of these two phyla. On the other hand, the presence of oxyhaemocyanin is not always easy to show for two reasons: first, because, while deep blue by reflected light, it is almost colourless by transmitted light, so that in small organisms its presence may be easily overlooked; second, because its presence may be marked, as is frequently the case with decapod crustacea, by pinkish or orange lipochromes, which are practically complementary. These being chloroform-soluble are easily removed. Blood of lobsters, crabs, snails, and Limulus which has been treated with chloroform will keep indefinitely in the cold, so that if a large stock of blood is prepared, it may be used for a long series of demonstrations. This is a very great advantage, since it obviates the necessity of bleeding animals for each experiment.

The methods appropriate to bleeding of snails, Limulus, and crustacea have been already described (*op. cit.*). The yield in the case of *Helix pomatia* is about 1·5 c.c. per individual; but as the blood can be diluted 50 per cent. for colorimetry, a considerable stock can be collected in about

two hours. In this country the crawfish is the most favourable material. To bleed the animal, first wipe and tie it fully extended to a stick. Then fix it vertically tail downwards over a suitable container, and remove the last abdominal tergite. The blood that oozes out during the first ten minutes should alone be used. Grind the coagulum with sand, and filter through muslin. Shake thoroughly the filtered serum with about one-fifth its volume of chloroform, and remove by the centrifuge the choloroform layer. Sufficient chloroform will be left in solution in the supernatant fluid to act as a preservative.

3. Apparatus Required.

For plotting a dissociation curve by this method the following equipment is essential: tubes of uniform bore (1·2 to 2·0 cm. diameter) for colour standards, a manometer, an equilibrating vessel fitted with tube of same bore as those used for colour standards, and a vacuum pump of some description. For more efficient working it is desirable to have a device for mechanical agitation while the sample of serum is brought into equilibrium with the required partial pressure of oxygen.

(*a*) *Colour Standards.*—For class demonstrations prepare colour standards by making 1 c.c., 2 c.c., 3 c.c. . . ., 9 c.c. of the serum up to 10 c.c. with the diluting fluid, adding additional tubes of diluting fluid alone and serum alone to complete the scale from 0 to 100 per cent. oxidation. For the diluting fluid, water made opalescent by addition of protein to match the reduced serum is used. If the reduced serum is of a yellowish tint a trace of neutral pigment to match reduced serum is substituted.

(*b*) *The Equilibrating Tube.*—Colour standards having been prepared, the remainder of the experiment is simple. Since it is not necessary to remove the blood from the vessel in which equilibrium is brought about, it is not necessary to prepare gas mixtures of known oxygen content in order to submit a sample of serum to a given partial pressure of oxygen. By connecting the equilibrating vessel with a rotary pump in circuit with a manometer the required pressure is established as indicated below. A convenient form of equilibrating vessel is seen in fig. 2. It is made by fitting into the neck of a separating funnel of about 150 c.c. capacity a tube of the same bore as that of the carefully selected tubes used for colour standards. The other end of the funnel fitted with a glass stop-cock is connected by pressure tubing with the pump when requisite, and protected by a rubber cap when immersed in the bath for making. About 10 c.c. of the serum is placed in the detachable tube into which the fluid drains when the intensity of the blue tint is compared with that of the colour standards.

(*c*) *The Manometer and Pump.*—A high-speed rotary pump greatly expedites working by this method, though with a good head of water-

pressure the use of a filter-pump (fig. 1) is adequate for the student's use. The manometer should be fitted with a water-trap in case careless use leads to a sucking backwards of the contents of the equilibrating vessel. To obtain any required oxygen pressure in the equilibrating vessel the latter is connected to the pump. The stop-cock of the equilibrating vessel is turned off when the required atmospheric pressure is reached. It is convenient for working purposes to have a stop-cock placed between the pump and manometer. If P is the partial pressure of oxygen required, M the difference in height of the mercury columns of the manometer, B the external atmospheric pressure, and V the vapour pressure of water at the temperature to which the sample is exposed,

$$P = 0{\cdot}21\ (B - M - V).$$

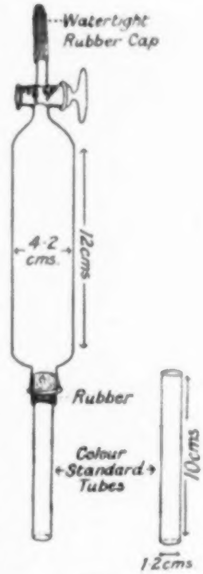

Fig. 2.

For rapid work it is desirable to eliminate arithmetical calculations during the course of the experiment, and hence it is advisable to mark off on the manometer scale the position of the mercury column corresponding to 5, 10, 15, 20, 30, 40, 50, 60, 80, 100, 120 mm. of oxygen pressure at 760 mm. atmospheric and zero vapour pressure. Approximately the same abscissal values are then used throughout all experiments, and the appropriate corrections for actual atmospheric pressure and vapour pressure of water are made at the end of the experiment.

(*d*) *The Shaker.*—The form of the shaker here suggested is adapted from a suggestion of Dr. A. C. Redfield on the lines of similar devices used in Barcroft's laboratory. The modification consists simply in permitting simultaneous shaking of five tubes adjusted to different pressures of oxygen. This makes it possible to execute a five-point curve from start to finish in about ten minutes.

The device consists of a solid brass base which stands (fig. 3) on the top of a water-bath into which a vertical plate dips down. The base carries a small motor ($\frac{1}{16}$th h.p.) driving a cogged wheel which sets in motion five cogged wheels inserted on the plate dipping into the bath. Each of these wheels carries a circular metal plate of the same diameter at the wide part of the equilibrating vessel. On each circular metal plate is inserted four strips of brass so that the equilibrating vessel can be inserted between them and held in position by a rubber band. Thus five equilibrating vessels

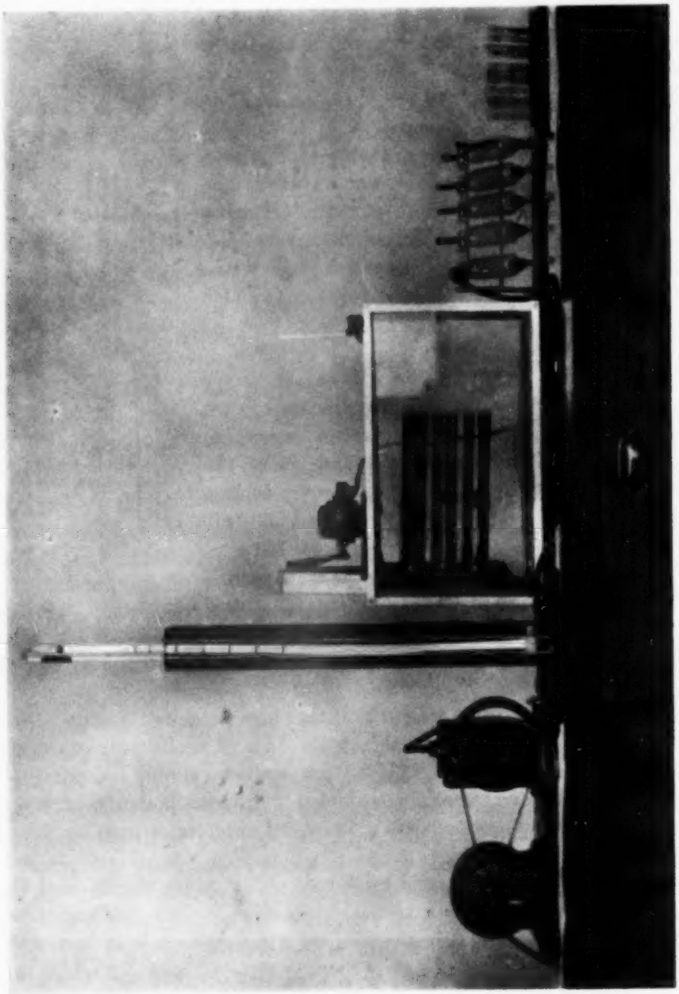

Fig. 3.

can be rotated simultaneously at the uniform temperature of the bath at any speed required to bring the serum rapidly into equilibrium with the gas pressure within the vessel.

4. Procedure.

A preliminary experiment carried out over a wide range of pressures, say 0, 10, 20, 80, 140 mm. of oxygen, will show once for all where the significant part of the curve for any sample lies, and the asymptotic character of the latter will make it evident that the blood is fully saturated at atmospheric partial pressure, *i.e.* that the normal serum used at the standard is 100 per cent. oxidised. Having adjusted the pressures in the sample tubes so that the points obtained will all fall on significant parts of the curve (as determined by previous experience), a preliminary mixing in the bath is generally adopted. The tubes are then tested to ascertain whether the pressure has remained constant. The fluid is allowed to drain into the lower portion, while air is instantaneously admitted and the original pressure restored. The object of this is to compensate for any error due to the giving off of oxygen by the blood itself, a source of error which in any case can be practically obliterated by making the air space in the manometer large. A second mixing is carried out for three minutes. The sampling tubes are removed and, after allowing the fluid to fall into the lower tube, are then compared with the colour standards. From start to finish the execution of a five-point dissociation curve does not require more than twenty minutes with the equipment described.

For experiments on the action of salts or of pH the blood should be dialysed in the cold.

The previous preparation of a large stock of blood by the chloroform method admits of a large number of experiments being done on the same sample of blood, *i.e.* a solution with uniform concentration of haemocyanin may be used throughout a series of tests.

For demonstrating the action of neutral salts the serum is diluted with an equal quantity of a solution twice the required concentration. The colour standards must be diluted in a similar manner with an equal quantity of *water* (not the diluting fluid, since the tint of the reduced serum will be paler owing to dilution). For demonstrating the influence of pH, add standard buffer solutions to different samples with water. The standards must be diluted in a corresponding manner.

In experiments on the effect of temperature well-buffered serum should be used and a different correction for vapour pressure applied at each temperature obtained by filling the bath with water of required warmth. The shaker can be lifted out of one bath into another at different temperature. Five minutes' final shaking after a preliminary shaking of ten minutes

suffices to achieve the requisite temperature equilibrium. For calculating results the following considerations apply:

If there exists a stoichiometrical relation such that l molecules of oxy-haemocyanin give rise to m molecules of reduced haemocyanin and n molecules of oxygen, then

$$\frac{[O_2]^n[\text{Red}]^m}{[\text{Oxid}]^l}=K.$$

If throughout a series of observations the same sample of blood, *i.e.* a solution of haemocyanin of the same molecular concentration, is employed as in all our previous experiments, and if x_{50}, x_{60}, . . . etc., be used to denote the oxygen partial pressure corresponding to 50, 60, etc., per cent. saturation, then by Henry's law,

$$x_{50}{}^n \propto K$$

and

$$n\, \partial \log x_{50}=\partial \log K.$$

If A represents a factor for solubility of oxygen at different temperatures,

$$n\,.\, d \log ax_{50}=d \log K.$$

Applying the Van't Hoff isochore

$$\log K=-\frac{Q}{2}\cdot\frac{1}{T}+c,$$

and putting $\tan \theta$ for the slope of the line obtained by plotting $\log_{10} ax_{50}$ against the reciprocal of the absolute temperature, we have

$$\frac{Q}{n}=2\times 2\,.\,303\,.\,\tan \theta.$$

This gives, as stated (Hogben, p. 230), a value for Q per gram molecule of oxygen. Opportunity may here be taken to correct an error overlooked on p. 238 (Hogben) and pp. 206 and 214 (Hogben and Pinhey) where the value of Q is referred to as the value per n gram molecules.

5. Summary.

An elaboration of the method proposed by Pantin and Hogben (1925) for studying the dissociation of the oxyhaemocyanins is here described. The new method makes it possible to plot a five-point dissociation curve

within a quarter of an hour with sera of Arthropods and Molluscs which can be kept indefinitely in the laboratory with prescribed precautions.

The general similarity in behaviour of haemocyanins and haemoglobins, the extreme simplicity of the method (even in the more elaborate form described below), and the importance of haemoglobin in physiological and biochemical teaching, justify the suggestion that the study of the haemocyanin system is a specially appropriate subject for laboratory work. Since a large yield can be obtained from such animals as *Maia* or *Limulus*, and since the blood of these animals, when filtered through muslin and shaken with chloroform, will keep indefinitely in the cold, no difficulty need arise in obtaining supplies through marine biological laboratories.

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A PRELIMINARY NOTE ON THE RHENOSTER BUSH (*ELYTROPAPPUS RHINOCEROTIS*) AND THE GERMINATION OF ITS SEED.*

By Margaret R. Levyns.

(With Plate XVII.)

There are six or seven species of Elytropappus recognised at the present time of which *E. Rhinocerotis*, the species under discussion, has by far the widest distribution. Sparrman, one of the most distinguished of the early South African travellers, refers to the spread of the Rhenoster bush as long ago as 1775. To-day the plant is still regarded as a pest by the farming community, and it is therefore a matter of some importance to have a detailed knowledge of its habits and life-history.

There is a popular impression, firmly implanted in the minds of many people, that the Rhenoster bush is an alien, and its rapid spread in places where man has disturbed the native vegetation is attributed to this cause. From a scientific point of view, however, there is no reason to suppose that when the native vegetation is destroyed, a native plant may not get out of hand in the process of recolonisation just as easily as one from some other country. All available evidence goes to show that South Africa is the home of the Rhenoster bush. In the first place, all the other species of Elytropappus are South African, and the genus itself belongs to a purely South African section of the Compositae. Further, there are no records of the genus in any other country.

Several distinct forms are included in the species as it is understood to-day. Some of these may eventually be given specific rank, but as Mr. J. Hutchinson of Kew is at present engaged upon a revision of the South African Compositae, the matter has been left in abeyance and specimens of the various forms have been forwarded to Kew for consideration. Two distinct types have been included in the present study (fig. 1 shows a shoot taken from each of these forms). When fully grown both are bushes from $2\frac{1}{2}$ to 4 feet in height ; they are of a grey-green colour and branch freely from the base. Type (*a*) is rather greener than type (*b*) and has a somewhat

* This work has been carried out with the assistance of a grant from the Research Grant Board.

stiffer habit of growth. The figure shows the shoots in full flower, and it will be noted that while in (*a*) the small capitula are densely clustered almost to the base of the branchlets, in (*b*) the capitula are borne in rather loose groups towards the ends of the slender branchlets. The capitula and florets are similar in the two forms, though in (*a*) the pappus is more strongly feathered than in (*b*). The colour of the pappus is brownish yellow in (*a*) and white in (*b*).

Type (*a*) is the form which is extremely common locally on Signal Hill, but there seems to be no definite records of it in any other place. However, the Rhenoster bush is poorly represented in herbaria (a fate which is probably due to its extreme commonness), and therefore the absence of records is certainly no proof that this form does not exist elsewhere. Type (*b*) has a much wider distribution and is the common form in the Stellenbosch, Malmesbury, and Worcester districts. It is present to a small extent on the Camps Bay slopes of Lion's Head, where it is found growing with form (*a*). For convenience of reference form (*a*) will be styled the Signal Hill type, and form (*b*) the Stellenbosch type.

The flowering season of the species is from April to June, and fruits may be gathered from June to August. These are borne in enormous numbers, giving the plant during the fruiting season a somewhat woolly appearance. Over 300 fruits were counted on an average twig 3 inches long, and as the plant is covered with such twigs, some conception of the output per plant may be gained. However, under 50 per cent. of the fruits appear to be fertile, which discounts to a small extent the extremely high rate of production. The fertile seeds in both forms show a surprising lack of structure. On dissection all that can be made out is an amorphous mass of food-reserve materials, protein and oil, and it is not until three or four days after the start of germination that the embryo assumes a definite form. The extremely light fruit with its feathery pappus is admirably adapted for dispersal by wind.

The information to be given in the following account has been derived from two sources :—

(*a*) Experiments under natural conditions at Ida's Valley, Stellenbosch.

(*b*) Experiments under artificial conditions in one of the greenhouses at the University of Cape Town.

Most of the Cape Town work was done with seed from the Signal Hill variety, but the Stellenbosch variety was also used during the early stages of the work. Identical results were obtained with the two forms, and therefore it was not considered necessary to continue using both.

Experiments under Natural Conditions.

The *raison d'être* of these experiments was the problem of veld burning, and a full account of the results obtained is in course of preparation. The present communication is concerned solely with the behaviour of the Rhenoster bush under the various conditions on the plots at Stellenbosch. The type of vegetation covering the plots before the start of the experiment was Rhenosterveld, which has been well described for the Stellenbosch district by Marloth in "Das Kapland." * This had not been burnt for at least sixteen years, a fact which gives added value to the experiments. Before the plots were touched one interesting and significant fact had come to light, viz. the Rhenoster bushes were all old ; dead bushes were to be seen here and there, and not a single seedling plant could be found. Seedlings of *Anthospermum aethiopicum* and a few other plants were frequently found. This points to the conclusion that in undisturbed Rhenosterveld the Rhenoster bush has no power of reproducing itself, and therefore must in time give way to other plants.

In April 1925 some plots were burnt, one was cleared of bush but otherwise left undisturbed, and one was left untouched as a control. Early in August screens were erected over small areas approximately 3 feet by 6 feet, one on a burnt plot and another on the cleared plot, so as to give about the same degree of shading as was present below the bushes on unaltered Rhenosterveld. Fig. 2 shows one of these shelters. It consisted of a roof of chicken wire supported on upright poles about 2 feet high. Branches of the Rhenoster bush were used for thatching purposes, and the light intensity was tested by means of a Watkins Bee Meter. Towards the end of 1925 Rhenoster seedlings were much in evidence on the burnt plots, as many as 694 being counted on one of the permanent quadrates 4 feet square. On the cleared plot a few seedlings were found here and there, while on the control plot not a single seedling could be seen. These results make it quite clear that apart from the removal of bush incidental to burning, fire definitely encourages the Rhenoster bush. Under the screens the seedlings showed clear signs of their inability to withstand shade. When the screens were erected the seedlings covered were of normal size, but five months later a marked difference was noticeable between exposed and shaded seedlings (fig. 3). To-day most of the seedlings under the screens are dead, and the few that remain are hardly likely to live much longer.

As soon as it became apparent that burning acted as a stimulus to seedling development, further experiments were designed to determine the factors at work. Two factors were considered : (*a*) the heat engendered at the time of burning, and (*b*) the action of the resultant ash from the bushes.

* Das Kapland, by Dr. R. Marloth (Gustav Fischer, Jena), 1908.

Unfortunately these experiments have given no definite results owing to an unforeseen factor which vitiated this part of the experiment, and which will be discussed in the next section of this paper.

Experiments under Artificial Conditions.

Large quantities of seed, chiefly from the Signal Hill form, were collected in June 1925, and during the winter months germination tests were carried out at the University of Cape Town. The seeds showed surprisingly low power of germination, as will be seen from the following table :—

No. of seeds sown.	Nature of soil, etc.	Percentage germination.
3000	Clay from Signal Hill.	4·0
600	Clay from Signal Hill, plus ash from burnt straw.	3·5
600	Rich potting soil.	27·0*
600	Clay from Signal Hill. Straw burnt over seed pans after sowing while seeds were still dry.	0·5
600	Clay from Signal Hill. Seeds sown 1 inch below surface.	1·0
600	Clay from Signal Hill. Seeds sown 2 inches below surface.	0·6†

In counting out the fruits for these tests only those were chosen which appeared to have a plump, well-developed seed inside.

The figures in the table indicate that burning straw over the seed pans and deep sowing of the seed tend to lower the percentage of germination.

Several seedlings were transferred to pots for further growth, and these were kept until they were five months old. By that time (November) the high temperature of the greenhouse during the day made continuance of the tests impracticable. The chief results may be summarised as follows :—

(*a*) The seedlings are exceedingly sensitive to lack of moisture, and unless the pots in which they are growing be kept standing in water, a hot, dry day kills off large numbers of seedlings.

* This unusually high figure is due to a 52 per cent. germination in one of the two seed pans. There was no obvious reason for this, as the other seed pan, apparently under exactly similar conditions, showed a germination figure just under 1 per cent.

† Three out of the four seedlings which appeared were growing round the edge of the pot, and therefore may possibly have arisen from seeds displaced when the covering soil was added.

(*b*) The plants grow much more rapidly in rich potting soil than in clay (fig. 4).

(*c*) The large plants in potting soil are very susceptible to attacks of aphis, whereas the plants grown in clay are not.

The author was away on leave during the late winter months of 1926, and it was only possible to make a few tests before leaving Cape Town. However, Miss E. McCullough, B.Sc., was kind enough to carry out some further experiments, and she obtained results of considerable interest, though the experiments must be extended before definite conclusions can be drawn from her results.

Both Miss McCullough and the author made sowings of seed gathered in 1925 and seed gathered in 1926, and the results of these tests are of considerable importance. The fresh seed behaved as in the previous year, while the old seed gave about 50 per cent. of germinations when grown on clay. When the old seed was grown on moist filter-paper in petri dishes the percentage was rather lower. This lowering of the percentage in water suggested further experiments, various solutions being used in place of water. Miss McCullough carried out these tests with seed gathered in 1925. Unfortunately only 20 seeds were used in each test, so that although the results are suggestive, further experiments will be needed before definite conclusions can be drawn.

	KNO_3.	$Ca(NO_3)_2$.	H_2O.	$MgSO_4$.	KH_2PO_4.	$Ca_3(PO_4)_2$
Number of germinations (20 seeds in each case).	9	8	4	10	12	12

Seeds gathered in 1925 and 1926 were sown on clay in earthenware saucers, and over these branches of Rhenoster bush were placed and then burnt. While no germinations were observed in the saucer with fresh seed, that with seed a year old showed an enormous crop of seedlings.

The conclusions to be drawn from the work in 1926 are—

(*a*) The seed needs a year's rest before germination.

(*b*) Seeds germinate better in various nutrient solutions than in water.

(*c*) While fire is detrimental to the germination of fresh seed, this is not so in the case of seed a year old.

The failure of several germination experiments at Ida's Valley, mentioned in an earlier part of the paper, was due to the fact that the tests were started

before it was realised that a year's rest for the seed is necessary. Consequently newly matured seed was used and no results have been obtained.

It is hoped to be able to continue these experiments, though owing to an unfortunate accident to the seed collected last year it will probably be necessary to wait until 1928.

a *b*

Fig. 1.—Two forms of "Rhenoster" bush, both found growing together on the Camps Bay slopes of Lion's Head.

(*a*) The characteristic Signal Hill form.

(*b*) The widely distributed form outside the Peninsula.

Fig. 2.—Light screen on one of the experimental plots at Ida's Valley, Stellenbosch.

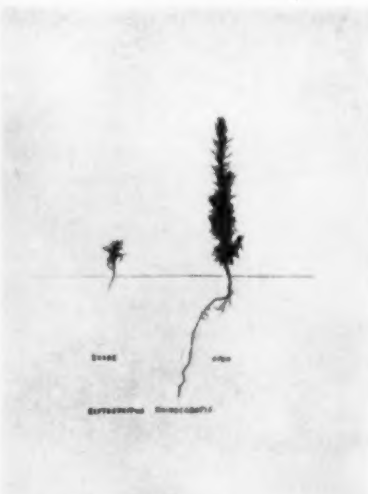

Fig. 3.—Two seedlings of *Elytropappus Rhinocerotis* grown on the experimental plots at Ida's Valley, Stellenbosch. Collected in December 1925; about seven months old. The large seedling was grown in the open on one of the burnt plots. The small seedling was grown on the same plot, but under a shelter.

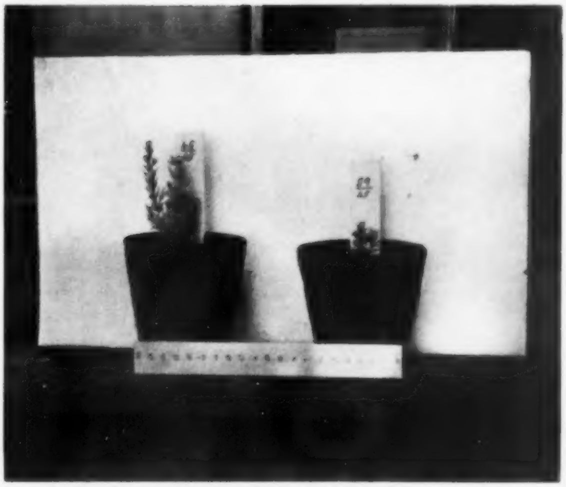

Fig. 4.—Two plants of *Elytropappus Rhinocerotis*. Both a little over three months old.

[illegible] grown in rich potting soil.

[illegible] grown in clay from Signal Hill.

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STUDIES IN THE GROWTH OF GRAPES.

Part II.—Relationship between Sugar and Acid in the Juice.

By P. R. v. d. R. Copeman, B.A., B.Sc.

(With one Text-figure.)

In a previous paper * a study was made of the changes which occurred during the ripening of grapes in the case of the acidity, sugar content, soluble-solid content of the juice, and of the total solids in the berry. It was shown that the time-relationships for the latter three quantities could be expressed by means of equations representing an autocatalytic change. The change in acidity could be expressed by means of an equation similar to one for a monomolecular reaction.

In all the work carried out in connection with the ripening of grapes it has been shown that the most important changes are those which take place in the sugar and acid-content of the juice. *During the ripening period* the sugar increases and the acid decreases. The remaining changes in the berry are completely subordinated by those which occur in these two factors. At maturity, the changes in the various factors become very small and practically negligible.

At the same time it could be clearly seen that there was a close relationship between these two factors such that a high content of sugar is associated with a low content of acid, and *vice versa*. It would appear that those conditions which favour the formation of sugar simultaneously favour a reduction in the acid content of the juice. These facts have been emphasised by other investigators. Caldwell, for example, in his paper † on "Some Effects of Seasonal Conditions upon the Chemical Composition of American Grape Juices," states that "there is a consistent and fairly high degree of correlation between sugar, acid, and total astringent content." Bioletti, Cruess, and Davi ‡ also draw attention to this fact and attempt to express this relationship by stating that "*during ripening* the sugar curve . . . is more or less the mirror image of the total acid curve

* Copeman, Trans. Roy. Soc. S. Afr., 1926.

† J. Agr. Res., vol. xxx, 1925, p. 1133.

‡ Univ. of Cal. Pub. in Agr. Sc., vol. iii, 1918, p. 103.

multiplied by five—*i.e.* increases as the acid decreases." There is therefore very little doubt that the relationship between the sugar and acid content of the juice is an inverse one. It will be shown, however, that the acid is not directly inversely proportional to the sugar.

As evidence of the close relationship between the acidity and sugar content of the juice the correlation coefficient between these two factors has been calculated for each variety. In each case the value was obtained by combining the experimental data obtained for each variety during the three seasons, 1923, 1925, and 1926. In addition, the data for both the Red and White Hanepoot varieties have been combined. The very close similarity in every respect between these two varieties and the fact that all the samples were obtained from the same locality (namely, Groot Constantia) justifies this step. Dr. Perold in his book * on Viticulture, states that these two varieties are identical in all respects except colour. He regards the Red Hanepoot simply as a "bud-variation" of the White.

The following correlation coefficients were obtained :—

Hanepoots	$-\cdot914\pm\cdot025$.
Gros Maroc	$-\cdot992\pm\cdot005$.
Barbarossa	$-\cdot914\pm\cdot038$.
Waltham Cross . . .	$-\cdot940\pm\cdot030$.
Flaming Tokai . . .	$-\cdot939\pm\cdot026$.

These values were calculated from the data obtained *during the ripening period*, *i.e.* while the acid was decreasing. They indicate a very high negative correlation, and their magnitude is the same for all varieties. The regression lines are not, however, linear, as can readily be seen by plotting the acid against the sugar. It can also be proved that the deviations from the line representing the direct inverse ratio are highly significant.

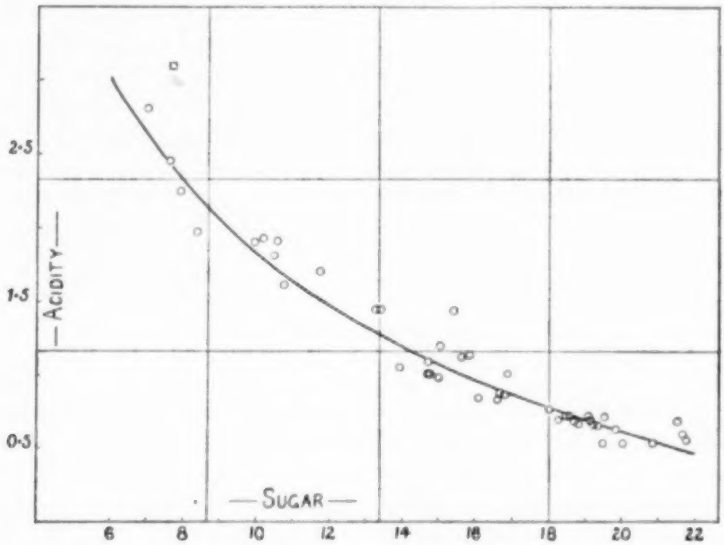
The type of curve showing the change of acid with sugar is shown in text-figure. The curve decreases as the sugar increases and is convex towards the sugar-axis. The values of the sugar content at the stage of initial decrease of acidity and the limit of maximum content of sugar vary slightly with the variety of grape. The present paper deals only with the data covered by these two stages.

In the previous paper † the curves for the time-relationships of the sugar and acid content are given separately. *During the period of decrease of acid* the change in acidity is given by

$$\log \frac{a}{y-a} = k_1(t-t'_1)$$

* Handboek oor Wijnbou, Stellenbosch, 1926, p. 283. † Copeman, *loc. cit.*

where y=acidity at time t.
a=minimum acidity or acid content of the juice at maturity.
t'_1=time when $y=2a$.
k_1=constant.



The change in the sugar content of the juice is given by

$$\log \frac{x}{b-x} = K_2(t-t''_1)$$

where x=sugar content at time t.
b=maximum sugar content of the juice.

t''_1=time when $x=\frac{b}{2}$.

$K_2=k_2b$=constant.

By eliminating t the following expression is obtained :—

$$\log \frac{\alpha a}{y-a} = \frac{k_1}{K_2} \log \frac{\beta x}{b-x} \quad . \quad . \quad . \quad . \quad (1)$$

where

$$\log \alpha = k_1 t'_1 \quad \text{and} \quad \log \beta = K_2 t''_1.$$

Equation (1) on simplification becomes

$$(y-a)^n = A_1\left(\frac{b-x}{x}\right) \quad . \quad . \quad . \quad . \quad . \quad (2)$$

or

$$(y-a)^n = \frac{A}{x} - B \quad . \quad . \quad . \quad . \quad . \quad . \quad (3)$$

where

$$n = \frac{K_2}{k_1}.$$

This gives an expression for the relationship between sugar and acid.

In practice, K_2 is dependent upon the magnitude of the total growth. In this particular case the period of growth is *limited to the period of decreasing acid*, so that under these conditions the total change in sugar content will be $b-s$ where s is the sugar content at the stage when the acidity commences to decrease. n, therefore, will be slightly less than the value given by

$$\frac{K_2}{k_1} \text{ or } \frac{k_2 b}{k_1}.$$

In determining the constants of equation (3) the equation was solved graphically for n by using the expression in the form

$$n \log (y-a) = C - \log x + \log (b-x)$$

when approximate values for a and b were chosen from the known values obtained from the separate time curves for sugar and acid. A and B were then corrected by the method of least squares.

The results obtained in this manner are given in Table I., in which are included the limits of sugar content for each variety between which the expression can be regarded as applicable to the data obtained.

Table I.

Hanepoots . .	$(y-{\cdot}35)^{1{\cdot}30} = \frac{29{\cdot}22}{x} - 1{\cdot}27$	from 6–22 per cent. sugar.
Gros Maroc . .	$(y-{\cdot}55)^{1{\cdot}45} = \frac{33{\cdot}76}{x} - 1{\cdot}65$	„ 5–20 „ „
Barbarossa . .	$(y-{\cdot}40)^{1{\cdot}20} = \frac{26{\cdot}00}{x} - 1{\cdot}32$	„ 6–19 „ „
Waltham Cross .	$(y-{\cdot}50)^{1{\cdot}23} = \frac{18{\cdot}28}{x} - 0{\cdot}87$	„ 5–20 „ „
Flaming Tokai .	$(y-{\cdot}45)^{1{\cdot}20} = \frac{29{\cdot}47}{x} - 1{\cdot}38$	„ 6–19 „ „

On account of the fact that the values for three seasons were employed, the values of the constants obtained will be the average of the values for each season separately. The agreement between the observed and calculated values is shown in the case of the Hanepoots in the figure. It can be shown that the deviations from the calculated results are not significant.

The lower limit for the sugar content represents the stage when the acid commences to exhibit a *definite* decrease, while the upper limit represents the average maximum development of the sugar content under *normal* conditions of growth. The variations in these factors and the total change of sugar content during this period are characteristic of each variety of grape.

In the expression a represents the minimum acidity of the juice, and its value is also characteristic of each variety. Since the results are calculated on the basis of three years' data it is clear that, under constant cultural conditions in one locality, the variations for any particular variety must lie within comparatively narrow limits. Consequently it may be concluded that the sugar and acid content of the juice do not fluctuate entirely independently of each other. Under these conditions it would seem that the factors which determine the chemical character of the crop are those which influence the photosynthetic activity of the plant. For example, any condition which favours the production of sugar must necessarily bring about a decrease in acid, the magnitude of which is related to the amount of sugar produced. These conclusions are in agreement with those drawn by Caldwell * in his paper.

For any particular variety of grape, then, it should be possible to predict with some degree of certainty the chemical character of the crop, provided that the same cultural conditions and the same locality are maintained. It follows that equable climatic conditions must, under such circumstances, tend towards the production of a uniform crop.

In the expression in the form (3), B represents the influence of a factor which is dependent upon the "grand period of growth." It is directly related to the value for the "half period" and its value is therefore characteristic of each variety. For example, an early ripening variety, such as Waltham Cross, has a low value for B, while a late ripening variety, such as Gros Maroc, has a high value. The value of $\frac{A}{B}$ is directly proportional to the maximum sugar value of the juice, as can be seen by comparing the values obtained, namely, 23·0, 20·5, 19·7, 21·0, 21·4 for the varieties in the order given in Table I.

In conclusion, the author would like to thank Dr. B. de C. Marchand for the interest he has taken in the preparation of this paper.

* Caldwell, *loc. cit.*

STUDIES IN THE GROWTH OF GRAPES.

Part III.—The Effect of Environment upon the Growth Constants.

By P. R. v. d. R. Copeman, B.A., B.Sc.

The value of employing some form of equation to express the changes which occur during the ripening of fruits depends largely upon the possibility of employing the constants so obtained as a means of expressing quantitatively the resultant effects of the conditions of growth. The type of equation to be chosen will therefore be one which most suitably fulfils this condition while, at the same time, agrees closely with the experimental data. Such equations need not necessarily be regarded as giving a complete picture of all the intricate processes involved in the growth of the plant. In the first paper * of this series the equations which were found to give the best expression to these ideas were worked out, in the case of grapes, for the changes in the acidity of the juice, the sugar and soluble-solid content of the juice, and in the total solids in the berry. Some of the consequences involved in adopting these equations were pointed out.

During the period of decrease of acidity, the changes in the acidity of the juice could be represented by the expression

$$\log \frac{a}{y-a} = k(t-t_1),$$

where "a" represents the minimum acidity at maturity and "k" the velocity constant of the transformation. The value of "k" would be expected to show variations according to the conditions under which the change takes place.

The curves obtained for the remaining three quantities are similar to the general reverse curves characteristic of growth in plants and animals, and this type of curve can be most suitably expressed by means of the equation for an autocatalytic reaction. Robertson † has developed this form of equation, particularly in respect of its application to the growth of animals, while other workers have employed it in the case of plants.‡

* Copeman, Trans. Roy. Soc. S. Afr., vol. xiv, 1927.

† Robertson, "The Chemical Basis of Growth and Senescence," Lippincott, 1923.

‡ For references, see Copeman, *loc. cit.*

Robertson stresses the fact that the very evident complexity of the growth processes constitute an obstacle to the acceptance of such a simple expression. However, he makes use of the idea that the complete process of growth must be dependent upon some "master reaction," which admits of representation by the autocatalytic formula.

The equation adopted to represent the changes occurring in the sugar content of the juice during the ripening of the berry was the simple autocatalytic expression

$$\log \frac{x}{b-x} = K_1(t-t_1),$$

where "b" represents the maximum amount of sugar formed under the conditions of growth, and $K_1 = k_1 b$, where "k_1" is the velocity constant of the change. According to Robertson's view the value of "b," the final resultant of the growth processes, is considerably influenced by environmental conditions, while "k_1" is regarded as a specific constant, representing inherent qualities of growth, and independent of environment. At the same time a high value of "K_1" is found to be associated with a short growing period, and is accordingly accompanied by a low crop-yield. Since "k_1" is directly proportional to "K_1," the value of "k_1" must vary in the same way. Under these circumstances it may be expected that "k_1" would show variations according to external conditions. This constant may be regarded as the *growth-velocity* constant of the plant. Conversely, $\frac{\text{“}b\text{”}}{K_1}$ will tend to vary directly with the crop-yield and is consequently better adapted for purposes of comparison. In this form it is a constant representing the *growth capacity* of the crop and may be expected to vary with environmental factors such as climate, treatment, etc.

In the case of the soluble solids in the juice and the total solids in the berry the type of equation which most suitably expresses the changes during growth in these two factors was found to be a modified form of the autocatalytic equation :

$$\log \frac{x-c}{d-x} = K_2(t-t_1),$$

where "c" represents the concentration of material necessary before the growth cycle represented by the above equation takes place. "d" represents the crop-yield of the berry as the final resultant of the complete growth processes. The crop-yield of the particular growth cycle under consideration is therefore "$d-c$." Under these conditions the *growth-velocity* constant of this particular cycle is $\frac{\text{“}K_2\text{”}}{d-c}$ and the growth-capacity constant is $\frac{\text{“}d-c\text{”}}{K_2}$.

As pointed out, it is to be expected that the values of the different constants should vary with the conditions of growth. Consequently they should possess some value as a measure of these variations. In the first paper * of this series the various constants for the above factors were worked out for six varieties of grapes obtained from Groot Constantia. The results for three separate years showed that the constants were characteristic for each variety, but that they varied within fairly narrow limits according to the variations in climatic conditions. It was felt, however, that results obtained for grapes from other localities would yield on comparison some useful information regarding the influence of environment upon the growth of grapes. The intention was to carry out parallel investigations on grapes obtained from both Paarl and Constantia, but circumstances, unfortunately, prevented the procuring of samples from Groot Constantia. However, since the variations in the constants for Constantia grapes for three widely differing seasons were not very large, it was felt that, by employing the mean values of the constants for these grapes, useful information could be obtained.

Since the main principles are applicable to all varieties of grapes, it was decided to employ only three varieties, namely, White Hanepoot, Barbarossa, and Flaming Tokai, as these offered examples of the most widely differing types of table grapes. The analyses were performed at weekly intervals on samples which were forwarded from the Paarl Viticultural Station through the kindness of the manager. The work was commenced on 4th December 1926 and continued until the end of March 1927. The early start was made in order to obtain some information which might assist in elucidating, if possible, the nature of the changes which take place in the very early stages of growth. The analyses were carried out in duplicate and the determinations were limited to the estimation of the acid, sugar, and soluble solids in the juice and the total solids in the berry. Mean values were taken for the purpose of calculating the constants of the equations.

The total rainfall during the period under investigation was 3·03 inches, of which 2·38 inches fell during February (mainly about the middle of the month). The average temperature during the same period was considerably higher than that which is usual at Constantia. The season, on the whole, was an unfavourable one. At the beginning of the season the weather was hot and dry, and it was only about the middle of February that sufficient rain fell to mitigate somewhat the ill-effects of the preceding dry weather.

In the case of the changes in the acid content of the juice, the initial period of increase was clearly marked and extended over a period of about six to eight weeks from the commencement of observation. As far as could

* Copeman, *loc. cit.*

be judged there was little evidence of zero acidity, and it is hoped to deal with this portion of the curve in a later paper. The form of equation already given was found to express very closely the changes in acidity which occurred during the period of decreasing acidity. In Table I the values obtained for the constants are given. The acidity was expressed as grammes of tartaric acid per 100 c.c. of juice, and the constants have been calculated exactly as in the previous paper.* For purposes of comparison the mean values of the constants for the same varieties of grapes from Constantia have been given.

TABLE I.—*Acidity*. $\log \frac{a}{y-a} = k(t-t_1)$.

Variety.	Locality.	a.	k.	t_1.
White Hanepoot	Paarl	0·40	0·0302	73·5
	Constantia	0·42	0·0230	..
Barbarossa	Paarl	0·40	0·0348	79·0
	Constantia	0·48	0·0283	..
Flaming Tokai	Paarl	0·36	0·0308	77·0
	Constantia	0·49	0·0281	..

On comparing the values of "a," the minimum acidity for Paarl and Constantia grapes, it will be seen that in the former case the values are slightly lower. This would indicate that the conditions at Paarl tend to favour a greater degree of ripening of the fruit. The differences for each variety are 0·02, 0·08, and 0·13 in the order given in the table, and these results seem to be connected with the order of ripening. In the early part of the season the climatic conditions were unfavourable, and apparently the change in the weather occurred in time to bring about a greater reduction in acidity in the two latter varieties, which are later ripening varieties than White Hanepoot.

In every case the value of "k," the specific velocity constant of the change, is distinctly greater for the Paarl grapes, and evidently the decrease of acid occurs far more rapidly in this locality than at Constantia. It is clear, therefore, that this constant is affected by environment, but there is no indication of how far it is influenced by any particular factor.

The value of "t_1," as given, does not form a suitable quantity for comparison since it is dependent upon the time at which the investigation is commenced. It indicates the fact that White Hanepoot ripens earlier than the other two varieties. If the time were taken from the point at

* Copeman, *loc. cit.*

which the acid commences to decrease, it would be found that the "half-period" value of the acid is reached more rapidly than at Constantia. This is in agreement with the higher value for "k."

In the case of the changes occurring in the sugar content of the juice it was found that, as in the case of Constantia grapes, the autocatalytic equation suitably expresses the changes. Distinct evidence of the effect of environment was found on comparing the values of the constants for these two localities. As in previous papers the sugar has been expressed as grammes of invert sugar per 100 c.c. of juice, and the constants evaluated as in the first paper * of this series. The values of the constants for Paarl grapes are given in Table II, together with the average values for Constantia grapes.

TABLE II.—*Sugar.* $\log \frac{x}{b-x} = K_1(t-t_1)$.

Variety.	Locality.	b.	K_1.	t_1.	k_1.	$\frac{b}{K_1} \times 10^{-2}$
White Hanepoot	Paarl	24·42	0·0258	68·5	0·00105	9·46
	Constantia	21·04	0·0387	..	0·00187	5·43
Barbarossa .	Paarl	19·50	0·0324	74·0	0·00166	6·05
	Constantia	17·78	0·0435	..	0·00246	4·08
Flaming Tokai .	Paarl	18·25	0·0303	70·5	0·00166	6·02
	Constantia	17·85	0·0454	..	0·00254	3·96

On comparing the values of "b" it will be seen that a greater value is obtained for Paarl grapes than for Constantia grapes, indicating a greater final crop-yield. From this point of view the conditions at Paarl would seem to be better adapted to the vine-growing industry. At the same time it will be noticed that the difference is greater with an early ripening variety such as White Hanepoot, and this would seem to show that the change in climatic conditions had some effect upon the growth of the berries.

As a result of the theoretical basis upon which these results are founded, it is to be expected that the value of "K_1" would show an inverse relationship to the crop-yield "b." In accordance with this assumption it will be seen that the value of "K_1" for Paarl grapes is distinctly less than that for Constantia grapes. It is clearly seen that a high crop-yield is associated with a low value of "K_1" and consequently with a long growing period, and it may be concluded that the development of the Paarl grapes is associated with a longer effective growing period. It is clear that the value of "K_1" is affected by environmental factors.

* Copeman, *loc. cit.*

Since $K_1=k_1b$ the same observations must be applicable to the values of the growth-velocity constant " k_1". It is clearly seen that this constant has a very much smaller value for Paarl grapes than for Constantia grapes, and it can only be concluded that this factor is distinctly affected by external conditions. Such a result would necessarily be expected from the point of view of chemical dynamics, since " k_1" represents the velocity constant of the transformation. Such a conclusion is in direct contradistinction to the views of Robertson,* who has based his arguments upon the similarity of the values of " k " obtained for British and Australian infants. It can only be concluded that the constancy of this factor in the cases he mentions is due to causes which do not operate in the case of plants. In the first place the evolution of the higher types of animals has been accompanied by an increasing perfection of the various mechanisms which are adapted to maintain constancy of the cell-medium. This factor would endow the higher types of animals with a greater resistance to changes in external conditions than is the case with plants. On the other hand, it may be that, with genetically related races, the various constants are subject to variations whose limits are extremely narrow. The results here obtained for grapes permit of no doubt that the velocity constant is affected by external factors. The explanation of Robertson's results must depend upon the existence of some mechanism which compensates the influences of environment. It would seem that Robertson has apparently overlooked the true significance of " k " in his argument. At the same time there is no doubt that *under comparable conditions* " k " is a constant which has a specific value for different varieties of plants, as is shown by the results for Paarl or Constantia grapes separately.

In accordance with the variations in the growth-velocity constant, the inverse factor $\frac{\text{"}b\text{"}}{K_1}$ or the growth-capacity constant is very much greater for Paarl grapes. From the point of view of the comparison between grapes grown in different localities it can be seen that this constant has a definite significance. It would be valuable to have a series of experiments indicating the value to be placed upon the influence of various external factors such as temperature, sunshine, etc., which would account for differences in the growth-capacity constant. The values of " t_1" are only useful as indicating the relative times at which the " half value " of the yield is reached for any one season. In point of fact the grapes develop slightly earlier at Paarl than at Constantia.

The same type of equation as used in the first paper † was found to be suitable for expressing the changes which occurred in the soluble-solid

* Robertson, *loc. cit.*

† Copeman, *loc. cit.*

content of the juice. The soluble solids were expressed in grammes per 100 c.c. of juice. In the present case this quantity was estimated from the specific gravity, which was determined by means of a specific gravity bottle after the juice had been filtered through filter-paper to remove suspended matter. The results were corrected to 20° C. and converted into soluble solids per 100 c.c. by means of tables. The results, obtained in this way, have been found to agree with the direct determinations well within the limits of experimental error. The values of the constants were calculated in the same way as before and are given in Table III, in which are included the values for Constantia grapes.

TABLE III.—*Soluble Solids.* $\log \frac{x-c}{d-x} = K_2(t-t_1)$.

Variety.	Locality.	c.	d.	K_2.	t.	k_2.	$\frac{d-c}{K_2} \times 10^{-2}$.
White Hanepoot	Paarl	4·75	26·82	0·0248	70·0	0·00112	9·00
	Constantia	3·85	23·48	0·0380	..	0·00196	5·11
Barbarossa	Paarl	4·65	22·15	0·0313	74·0	0·00180	5·60
	Constantia	3·50	20·26	0·0413	..	0·00247	4·06
Flaming Tokai	Paarl	4·80	21·05	0·0301	73·0	0·00186	5·40
	Constantia	4·33	21·38	0·0426	..	0·00250	4·00

On comparing the values of "c" with the values for Constantia grapes, it will be seen that in the present case the values are greater. Therefore the commencement of this cycle of growth must occur at Paarl at a stage when there is a greater concentration of soluble solids in the juice. The final crop-yield, as represented by "d," is greater in the case of White Hanepoot and Barbarossa, but approximately the same in the case of Flaming Tokai. This result may possibly be due to the fact that the latter is a late ripening variety, and owing to the change in climatic conditions, resulting in more favourable weather, the ripening process was accelerated with the resulting tendency towards a lowering of the crop-yield.

In every case the value of "K_2" and "k_2" were distinctly lower than the corresponding constants for the Constantia grapes and are evidence of the conclusion that these growth constants are definitely affected by environment. The lower values indicate a longer period of effective growth at Paarl, so that the fruit attains a fuller development. In accordance with this view the values of the *growth-capacity* constant are greater for the Paarl grapes. It will be seen that the greatest change takes place in the value for White Hanepoot, which has been increased by nearly 80 per cent.

The close relationship between the changes in acid, sugar, and soluble solids in the juice is shown in Table IV, where the constant K_2 for the soluble solids is calculated from the constants for the acid and sugar separately by means of the expression

$$K_2(a+b)=K_1b+ka,$$

where the symbols have the significance already attached to them.

TABLE IV.

	K_2 (obs.).	K_2 (calc.).
White Hanepoot . .	0·0248	0·0249
Barbarossa . . .	0·0313	0·0305
Flaming Tokai . . .	0·0301	0·0297

Finally, the type of equation suitable for expressing the changes which occur in the total solids in the berry resembles that for the soluble solids in the same way as in the case of Constantia grapes. The total solids were expressed in terms of grammes per 100 grms. of berry, and the constants in the same way as before. The values for Paarl and Constantia grapes are given in Table V.

TABLE V.—*Total Solids.* $\log \frac{x-c}{d-x}=K_3(t-t_1)$.

Variety.	Locality.	c.	d.	K_3.	t_1.	k_3.	$\frac{d-c}{K_3}\times 10^{-2}$.
White Hanepoot	Paarl	6·12	25·62	0·0231	66·5	0·00118	8·44
	Constantia	5·88	23·25	0·0326	. .	0·00185	5·42
Barbarossa	Paarl	6·45	21·50	0·0259	70·5	0·00172	5·81
	Constantia	6·14	21·45	0·0333	. .	0·00218	4·59
Flaming Tokai .	Paarl	6·75	22·55	0·0261	68·5	0·00166	6·02
	Constantia	7·90	22·46	0·0348	. .	0·00239	4·19

On plotting the results for the Paarl grapes, it was seen that the total solids decrease initially to a minimum value before the increase, corresponding to the growth cycle here given, becomes evident. This minimum value is represented by "c" grammes per 100 grms. of berry, and it would therefore seem that in the initial stages of formation of the berry

the main process must be an absorption of water. This process is initially very rapid, and any *possible* formation of solids is completely masked. There is some slight evidence that a similar effect exists in the case of the soluble solids, but it is not so clearly defined. In neither case is it possible to define the exact course of the change.

In the case of the various constants obtained for the normal growth cycle in Paarl grapes the same remarks are applicable as in the case of the constants for the soluble solids. The close relationship between these factors is indicated by the magnitude of the constants in the two cases. It is clear that the changes in the total solids are almost entirely dependent upon the changes in the soluble solids. The value of the velocity constant is practically identical in both cases, and the influence of external environmental factors is clearly evident.

All the facts so far elucidated show that the growth constants for the various factors are all influenced in the same way, so that the effects due to a change in environment are not confined to a single factor. The changes in the growth constants are all, to an equal extent, significantly affected by changes in environment. When the values of the constants are considered for each locality separately, it will be seen that they are genetically significant for the different varieties and are of value from this point of view. It is clear, however, that environment directly influences these factors in the case of plants, and so far as Robertson's work on animals is concerned it can only be concluded that some mechanism must exist which tends to counteract the effects due to changes in environment. As a means of comparison between varieties of grapes grown in different localities, the growth-capacity constant may yield useful information.

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ON THE HERPETOLOGICAL FAUNA OF THE LOBATSI-LINOKANA AREA.

By J. H. Power.

(With a Map, Plates XVIII–XXII, and one Text-figure.)

Part I.—Lobatsi, 25° 8′ S., 25° 43′ E.

Introduction.

The first excursion to the above neighbourhood was made in 1924; the results proved so interesting that each succeeding year the visits have been continued.

The author's best thanks are due to the Research Grant Board, without whose assistance these expeditions would not have been possible.

The topography of this area (see map) is sufficiently interesting to deserve a short account:

After leaving Mafeking the country for miles is absolutely flat with no sign of hills from horizon to horizon; then hills begin to appear to the north. These are the Linokana Hills and extend from the west of Lobatsi to the east of Linokana.

From being low, hazy specks on the horizon these gradually loom up until eventually, on passing through a narrow gap (see Pl. XVIII, fig. 1), the basin-like valley of Lobatsi breaks on one's view with dramatic suddenness.

The little village nestles in a pretty, almost circular, valley among the hills. The road from Lobatsi to Linokana, a distance of over 23 miles, lies in a valley between two ranges of hills; the mean width of the valley is 1½ miles.

The hills and kloofs surrounding Lobatsi and Linokana, together with the valley connecting the two, is the area collected (see map).

The author's headquarters while in the Lobatsi area were at the railway station. He had access to three distinct types of habitat:

1. The hills, some of which have very little vegetation, while others are covered with aloes and various trees and shrubs, are mostly dolomite and quartzite formations, and in some cases have precipitous sides.

2. The grassy valleys in which flourished various species of Acacia,

some of them growing to a height of 40 feet or more. These trees grow in clumps, giving the valleys a park-like aspect (see Pl. XVIII, fig. 2).

3. The dams and pools, the edges of which, except in the case of rock-bound ones, are covered with reeds and sedges.

These three habitats had each its particular fauna.

Lacertilia.

Pachydactylus capensis, Smith.

This species is, apparently, not very common as only one specimen was secured. This was found under a stone on the foothills.

Agama hispida distanti, Boul.

Two specimens of this species were taken; they show a very rough dorsal scaling similar to specimens from Otto's Hoop (**1**). Other specimens were seen on the fence posts and on stones, but always on the flats. The species is evidently fairly common.

Agama atra, Daud.

This is the dominant form in the hills and kloofs where it may be seen on the tops of jutting rocks. Several specimens were collected and presented to the M'Gregor Museum, Kimberley.

Agama atricollis, Smith.

This lizard is decidedly arboreal in its habits; the rough bark of the Acacias gives it an admirable climbing surface. This Agama was never noticed away from trees. The colour so assimilates the grey tint of the bark that the creatures are very difficult to see; this, together with the uncanny ease and rapidity with which they slip round to the side of the branch opposite to the observer, renders them quite difficult to collect. The seven specimens taken were all shot from branches of trees sometimes as high up as 20 feet. The stomach of a large male contained an almost complete specimen of *Sternocera orissa*, with several fragments of species of *cetoniids*. These beetles frequent the trees and are probably captured high up among the branches.

The largest male of this Agama collected reaches a total length of 343 mm., being 150 mm. from snout to vent. The head is triangular, measuring 48 mm. at the base, then tapering suddenly to a point at the snout. The females are much smaller, being only 278 mm. total length,

and 128 mm. from snout to vent. The male has usually three rows of preanal pores.

Zonurus jonesii, Boul.

This species is plentiful on the hills; it seems to have a preference for the dolomite kopjes where the profusion of cracks and crevices gives it ample means of retreat in case of danger.

Zonurus vittifer, Riech.

Only one specimen of this lizard was secured; it is evidently rather scarce, certainly by no means as plentiful as *Z. jonesii*.

How the species distribute themselves the author cannot say, but it is noteworthy that the only specimen seen was taken in a small thorn tree about 4 feet from the ground. According to van Dam (**19**), it frequents only the rocky kopjes in the neighbourhood of Pretoria.

Varanus albigularis, Daud.

Fairly common on the flats and in the dry dongas; one juvenile specimen was secured.

Varanus niloticus, Linn.

This species is said to occur in the marsh lands and permanent pools; no specimens were seen by the author.

Nucras intertexta, Smith.

One specimen collected agrees with Boulenger's key (**2**) for the above species, save in respect of the head which is considerably broader than deep. The pattern agrees with that of Plate vii, fig. 3 (**2**). It is noteworthy that another specimen in the M'Gregor Museum from Molopololi (about 55 miles north-west of Lobatsi) is exactly similar to the Lobatsi one.

This swift-running lizard is fairly common on the flats among the tufts of grass.

Ichnotropis squamulosa, Peters.

This small lizard is extremely active and often difficult to capture even when wounded. When disturbed it dashes off with arrow-like swiftness, but seldom goes further than from 5 to 7 yards before it stops.

Invariably it runs to a clump of grass or scrub for protection, hiding on the opposite side from the pursuer.

This habit of dashing off to a distance when disturbed makes it by no means easy to collect, besides, it stops so abruptly that it is often difficult to locate it.

Its colour is an additional advantage to it for it much resembles the red earth.

It is one of the commonest lizards of the region, but is confined to the sandy flats. Several specimens were collected and are now preserved in the M'Gregor Museum, Kimberley.

Gerrhosaurus flavigularis, Wiegm.

Quite a common lizard in the hills and on the foothills. Four specimens were collected; some on the foothills and some on the tops of the highest points.

One of these specimens is worthy of note, inasmuch as it has the fronto-nasal separated from the frontal by a broad suture between the prefrontals as in the case of *nigrolineatus*. This is evidently not unusual as Hewitt (**8**), speaking of the material in the Transvaal Museum, says: "Our series of *G. flavigularis* shows much variation in the relationship of the fronto-nasal to the neighbouring scutes; it is always shut off from the rostral, but it may form a broad or a very narrow suture with the frontal; or *not infrequently the prefrontals may form a broad median suture.*" *

The other characters, used to separate *flavigularis* from *nigrolineatus*, also vary considerably and result in much overlapping, so that it is very doubtful, in the light of present-day material, whether the latter deserves more than varietal rank. See also Hewitt (**5**).

Mabuia trivittata, Cuv.

This species is by no means as plentiful as it is further south, say at Kimberley.

Only one specimen was secured and very few seen.

Mabuia striata, Peters.

So common in the neighbourhood of human habitations at Kimberley, it is very scarce at Lobatsi. Three specimens only were observed on the flats; one was shot on a fence post.

Mabuia varia, Peters.

This is the commonest lizard of the region. It inhabits the foothills and is an extremely active little creature.

The characteristic sharply defined whitish lateral streak, starting on the upper lip and passing through the ear, is present in all the sixteen specimens collected. One gravid female contained eight embryos.

* The italics are those of the present author.

Chamaeleon quilensis, Boc.

This chamaeleon is quite plentiful in the wooded valleys over the whole area. Many specimens were taken both on the ground and in the trees.

Ophidia.

Python sebae, Gmel.

This, our largest snake, is occasionally met with; as a rule, it inhabits the steep mountain-sides, but is also found in the valleys. One juvenile specimen was taken.

Philothamnus semivariegatus, Smith.

Occurs in the bush in all the valleys and on the foothills. This is a typical tree snake, its colouring being so protective that it is extremely difficult to see in the bush. In no case was an individual noticed until attention was called to it by its movements, and in many cases, even after the creature was located, it glided away quickly to another part of a bush and was lost sight of again.

This snake does not resent handling; after the first fright of capture is over, it never attempts to bite.

Psammophis subtaeniatus, Peters.

The South African representatives of this genus are badly in need of revision for the systematic position of certain species is not at all clear.

In 1896 Dr. Boulenger (**3**) separated the greater number of the species of *Psammophis* into three groups according to the character of the rostral, putting *bocagii* in the deep rostral section. In 1910 he included this species under the heading rostral considerably broader than deep. In any case the shape of the rostral is variable.

Psammophis subtaeniatus was originally described by Peters (**13**), in 1882, as a variety of *sibilans*; while *P. bocagii* was first described as variety (A) of *P. sibilans* by Bocage (**5**) in 1895. Hewitt (**10**) considers *bocagii* and *transvaalensis* synonyms of *subtaeniatus*.

From the above it would appear that the name *subtaeniatus* may stand, and the Lobatsi specimens are referred to this species. The table on next page gives the particulars of the two specimens taken.

This snake was found only in the hills; one specimen shot was in the act of eating a frog.

Locality.	No. of Upper Labials.	No. of Labials entering the Eye.	Ventrals.	Praeocular and Frontal in Contact.	No. of Praeoculars.	Character of Rostral.	
Lobatsi	9	3	169	Ne.	2	0	0=broader than deep.
Lobatsi	9	3	168	Ne.	2	Δ	Δ=deeper than broad.

Trimerorhinus tritaeniatus, Günth.

This snake occurs both on the foothills and in the valleys, but is not common ; only two specimens were seen.

Thelotornis kirtlandi, Hallow.

Although this species was not met with by the author, from information given by the inhabitants he is of opinion that it probably occurs in the bush round Lobatsi.

Naia nigricollis, Reinh.

This is by far the commonest snake of the area, for, although only nine specimens in all were secured, many more could have been collected. It seems to have a preference for the neighbourhood of human habitations and is consequently very dangerous. One large specimen was killed on the verandah of the hotel, others near the native huts.

Chelonia.

Cinixys lobatsiana, n. sp.

(Plates XIX and XX.)

Description based on Three Adults and One Juvenile.

Anterior and posterior margins of carapace reverted and dentated, the former slightly, the latter strongly so ; a narrow nuchal shield ; shields concentrically grooved ; vertebrals generally as broad as the costals.

Hinge between the seventh and eighth marginal, the second and third costal, the third and fourth neural shields. Posterior part of the carapace sloping. Plastron with thick anterior lip which is notched and projecting beyond the carapace, the length of the gular shield nine times into the total length ; caudal shield short, very openly notched, its width half the width of the bridge. The longest median suture is between the abdominal

shields, which equals two and three-quarter times that between the pectorals; the smallest shields are the gulars. Inguinal large, axillary very small and divided.

Carapace uniform reddish brown or yellowish brown; plastron uniform yellowish. The one juvenile specimen had scales yellowish brown in the centre, becoming reddish brown towards the outer margin; dark splashes or rays on the outer half of each scale.

All-over length of shell	14·7 centimetres.	♂.
,, ,, ,,	16·1 ,,	♀.
,, ,, ,,	12·5 ,,	juvenile.

This species is nearest to *C. erosa*, from which it differs in the presence of a nuchal shield. It differs from *C. homeana*, in that the plastron projects beyond the carapace anteriorly, and the posterior part of the carapace is sloping.

All the specimens collected were found in the kloofs among the hills; one was found eating a mushroom.

Pelusios sinuatus, Smith.

Numbers of water tortoises were seen, but unfortunately the author was unable to secure a specimen. However, from observation he supposes them to be referable to the above species. Every permanent pool and dam had some of these creatures.

Batrachia.

Rana oxyrhynchus, Smith.

This frog is found in abundance around Lobatsi. An account of the habits and life-history is at present in the press (**14**); to this the following additional note is now added :—

The eggs are also laid in masses, very similar to the egg-masses of *Phrynobatrachus natalensis* which float on the surface, or they may be attached in a mass to weeds at the bottom.

Pyxicephalus adspersus, Tschudi.

This species was not observed, but the inhabitants are quite emphatic as to its occurrence in the neighbourhood. The following account of the metamorphosis is drawn up from observations made at Kimberley :—

Eggs to the number of approximately between 3000 and 4000 were found lying on the bottom in very shallow water, near the edge of a pool, on the morning of 18th December 1926. They had probably been laid the previous night.

They measured 2·0 mm. in diameter; the capsule measured 4·0 mm. The upper pole is black, the lower dirty white; the capsule is highly musci-laginous, consequently the mass had a lot of foreign matter adhering to it, thus rendering it difficult to see.

By the following morning (19th December 1926) the larvae had hatched and measured 4 mm. total length. They were still within the egg-capsule and were jet-black, save in the abdominal region, which was deep sepia colour.

On 20th December 1926 they had left the capsule and were adhering to the outer surface; large branching external gills had developed. It was noted that the tadpoles swam on their backs at this stage when they moved. They measured 7·5 mm. total length, tail 5 mm. The eyes were now developed and the mouth being formed.

On 21st December 1926 they were very active, swimming about on their backs or clustering in the corners of the tank. The external gills, though visible, were fast disappearing; the gut and mouth were now formed. The tail-fin showed exceptional development at this stage. Total length 9 mm., tail 6 mm.

On 22nd December 1926 the external gills had entirely disappeared; the gut and cloacal tube contained food; the beak and horny teeth were visible. The positions occupied by the adhesive apparatus and external gills were indicated by dark patches; the spiraculum was not yet visible. Total length 11 mm., tail 7 mm.

On 23rd December 1926 the spiraculum became visible; the legs began to appear. They were now feeding from the sides of the aquarium and from decaying vegetable matter therein.

On 31st January 1927 they reached their greatest length, 71 mm. total, tail 43·5 mm.

On 2nd February 1927 the arms, first the left through the spiraculum, came through. The tailed frogs left the water on 5th February 1927, and two days later the tails had entirely disappeared; the tiny frogs at this stage measured 22·5 mm. from snout to vent and possessed the characteristic folded skin of the adult.

Colour.—The tadpoles were jet-black from the time of hatching up to about a week before the arms came through, when they assumed an olive colour. The young frogs were a bright green with a yellow vertebral stripe.

The tadpole has already been described (**14**).

Pyxicephalus delalandi, Tschudi.

This species is very plentiful and, after rain, larvae may be collected in abundance in any muddy pool. Ten specimens were taken, but this by no means indicates how plentiful this frog is.

Tadpoles of this species collected at Lobatsi show no variation from those collected at Kimberley, but some taken on the seashore at Fish Hoek, C.P., showed not a vestige of horny teeth; the beak was well developed.

Phrynobatrachus natalensis, Smith.

This is quite a common frog in the Lobatsi neighbourhood and may be heard calling during the day and night, in the breeding season, at almost every pool.

Fifteen specimens were taken, but many more could have been collected.

Cassina senegalensis, Dum. and Bibr.

This frog may be heard calling during the late evening and night in great numbers at every pool in the breeding season, especially after rain. The following notes are added to those already published (**15**):—

When the embrace has taken place the pair sit near the edge of the pool until the female is ready to deposit some eggs, which is usually from an hour to two hours after pairing takes place. She enters the water and swims a short distance from the edge, then dives to the bottom where she grasps a leaf, piece of straw, stick, or other object with her hands, at the same time bringing forward the anal aperture until it touches the object grasped; an egg is now extruded and attaches itself by its highly glutinous capsule. It loses its glutinous quality almost immediately after being laid. This operation is repeated until about 5 or 6 eggs are laid, when the pair swim to the shore and the female rests for a short time before continuing operations. This goes on throughout the night and into the early hours of the morning until from 100 to 200 eggs are laid. The egg is attached to plants, etc., by fibrous-like strands; it is encased in a single capsule which is entirely different from the egg-capsule of any other frog known to the author. It is hard and of a semi-transparent yellowish-brown colour, having a rough, granular-looking outer surface; it offers resistance to fairly strong pressure. When broken and the egg removed, it resembles in consistency the husk of a pepper berry; the fractured edges have a fibrous appearance when seen through the microscope. In fact it is a rudimentary egg-shell.

Twenty of these egg-shells were removed and handed to Mr. John Parry of De Beer's Laboratory for analysis. The following is his report thereon:—

"Air-dried shells from twenty frog's eggs. Weight ·005 grm.

"On ignition at 201° C. there was left a brown residue weighing ·0004 grm. Loss, therefore, was ·0046—that is, 92 per cent.

"The material left was treated with hydrochloric acid in which it

dissolved, partially, and gave reaction for a minute trace of lime (CaO), and also a faint trace of iron."

Bles (**7**) describes a somewhat similar capsule enclosing the egg of *Xenopus laevis*, but the present author has compared the egg-capsule of both these anura and finds that of *Cassina* much harder. Bles states that the outer coat of the egg of *Xenopus* shrinks into a shrivelled ring when the larva leaves it ; this is not so in the case of the shells of *Cassina* eggs, they retain, more or less, their rigidness. The larva of *Cassina* reaches a much

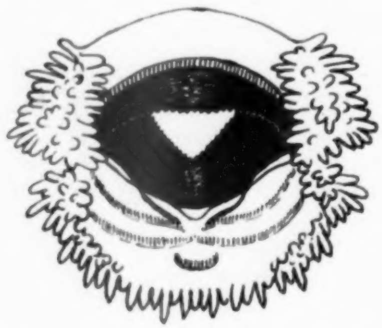

FIG. 1.—Mouth-disc of the tadpole of *Cassina wealii* from the Cape Peninsula.

more advanced stage of development within the egg-shell than that of *Xenopus*.

The tadpole has already been described (**15**). Noble (**12**) calls attention to the shape of the upper lip and the presence of a black horny plate which lies obliquely on either side and slightly below the lower mandible in the tadpole of this species, and says : "In recently examining the amphibian collections in the Berlin Museum, I found some tadpoles from East Africa attributed to *Hylambates maculatus*. These tadpoles exhibited the same features described above." He then goes on to point out that this would seem to indicate a relationship between *Hylambates* and *Cassina*.

There is scarcely a doubt that the Berlin Museum specimens are those of *Cassina* sp. Noble's fig. 1*b* exactly resembles the mouth-disc of tadpoles of *Cassina wealii* from the Cape Peninsula (see fig. 1). In the same paper (page 3) he points out Wager's mistake in concluding that certain tadpoles taken in a pool must be *Rappia* larvae, because this was the only frog heard calling there. The collector of the Berlin Museum material is most probably guilty of the identical mistake.

A curious case of abnormal development of the tail-fins of the tadpoles has already been noted (**17**).

Cacosternum boettgeri, Boul.

Only three specimens of this species were taken ; it is by no means as plentiful at Lobatsi as it is further south. Probably Lobatsi is near its north-central boundary of distribution.

Phrynomerus bifasciatus,* Smith.

This remarkable frog is plentiful at night in the breeding season ; twelve specimens were secured, but many more could have been collected.

The following additional notes on its habits and life-history are added to those already published (**15**).

Several masses of newly laid eggs were found in a small dam on the morning of 10th December 1926 ; these were either resting on plants or lying on the bottom in shallow water near the edge. If they are not supported by some object they instantly sink ; each mass contains from 1000 to 1500 eggs. The egg measures 1·3 mm. in diameter and is enclosed in three jelly-like capsules, the outer of which is highly mucilaginous and has a diameter of 4–5 mm. The upper pole of the egg is light brown ; the lower, white.

On the morning of 12th December 1926 the eggs had hatched, and on the following day the larvae, still within the egg-capsule, measured 4 mm., tail 1·5 mm. ; the outer capsule at this stage measured 7 mm. in diameter.

On 14th December 1926 the larvae left the capsules. It may be stated here that the eggs were kept in tins on a verandah away from any direct sunlight. Probably in their natural state they hatch much quicker.

The author was fortunate in securing a large collection of tadpoles of this species (some hundreds of specimens) in all stages of development. Some of these had almost completed their metamorphosis when he arrived at Lobatsi early in December, which means that the eggs must have been laid early in October. Loveridge (**18**) found this species breeding at Kilosa in April ; thus the breeding season would probably be from the end of September to the end of April.

The following are additional notes on the tadpole which has already been described (**15**) :—

The lower crest of the tail is only one-third deeper than the upper in more advanced specimens with well-developed legs.

Quantities of the tadpoles can be collected with each dip of the net ; several were caught on 13th December 1926 and taken back to Kimberley alive, and allowed to complete their metamorphosis. The largest of these measured 35 mm., total length, with fairly well-developed legs.

* This new name, suggested by Noble, is necessary in view of his discovery that the Amboyna species cannot be maintained in the same genus as the African ones.

The arms of the most advanced specimens came through on 24th December 1926, and the little frogs left the water on 26th December 1926, the tail being almost completely absorbed. The young frogs averaged 12 mm. from snout to vent; one specimen reached 14 mm. The colouring is most unlike that of the adult, being silvery grey above, with a black stripe down the centre of the back from between the eyes to the legs and having a fine orange line in the centre. There is also a short narrow orange line on the back between the legs. The sides are black as are also the arms and legs, the latter being barred with silvery grey. Beneath the head is a dark smoky colour; the remainder of the ventral surface is white.

Speaking of the young of this species seen in East Africa, Loveridge (**18**) says: "They lacked the gaudy red markings of the adults, and this is just when one would assume that they most stood in need of their 'warning colours'; they were brownish, with the pattern showing more distinctly than in the adults."

This infers that the colours of the adult are warning colours, though as far as the author is aware this has never been proved.

Bufo regularis, Reuss.

This toad is fairly common although not so plentiful as *Bufo carens*. It is interesting to note that these two species were found pairing in two different pools, but, owing to the great numbers of *B. carens* in such pools, it was impossible to secure eggs. A search for hybrids resulted in the discovery of only two in many thousands examined. These have been described and figured (**16**).

Bufo regularis gutturalis, n. subsp.

(Plate XXI, fig. 2.)

Early in January 1926 the author visited Lobatsi on one of his field expeditions. One night succeeding a thunder shower an unknown anuran call was heard; on proceeding to the spot from whence it came, about fourteen toads were found (ten of which were captured and brought to Kimberley) calling lustily within an area of about 8 square yards. They gave vent to a guttural sound which resembled very much the call of the Blue Crane (*Tetrapteryx paradisea*). No breeding pairs were found, nor were any females noticed in the vicinity. It was noted that, while these unknown toads occupied that part of the pond where short water-weeds were plentiful, *B. regularis* remained at the opposite end where there were no weeds but an open muddy stretch of 4 or 5 yards. Several males of *B. regularis* were also calling, the notes being no different from those of

the species heard by the author in other parts of the Union. The fact that the two lots of toads were so close and yet did not associate, together with the extraordinary difference in the calls, convinced the writer that they must be distinct species. The call of the unknown toad, besides being totally different from, was also much louder than that of *B. regularis*.

It seems to the author that such an important factor in the mating of anura as the call of the male, even if it differs but slightly, must give rise to a new group. A later examination of the material showed that this toad did not fit in with any of the species recorded from South Africa. It was thought at first that it might be *B. tuberculosus*, Bocage (**6**), since the type of that species came from Linokana, only 23 miles away, but it differs from Bocage's description in the following respects :—

In the length of the major axis of the tympanum as compared with the width of the upper eyelid ; in the proportions of the parotoids, longer and narrower in *gutturalis* ; in the more slender fingers ; the webbing of the toes ; the character of the inner metatarsal tubercle and the granulation of the ventral surface.

It is near *B. regularis* (see Pl. **XXI**, fig. 1), from which it can be distinguished by the much more slender fingers and toes, which in the case of *gutturalis* are, as a rule, tipped with a dark brown horny excrescence ; this applies to both sexes. The webbing of the toes not prolonged to the extremities as a border.

Dorsal tubercles not as large as is usually the case in *regularis* ; each tubercle having a horny spine ; parotoids much smaller and narrower, slightly more than twice as long as broad in *regularis*, three times as long as broad in *gutturalis* ; the smaller size of the adults, average of thirty specimens of *regularis* 88 mm., snout to vent, of thirty specimens of *gutturalis* 77 mm.

The following description is drawn up from four specimens preserved in the M'Gregor Museum, Kimberley ; a male and female from Lobatsi and a male and female from Kuruman :—

Head moderately large, snout short and rounded ; nostrils nearer the end of the snout than the eye ; the distance which separates them shorter than the distance to the edge of the jaw. Interorbital space flat, narrower than the length of the upper eyelid. Tympanum oval or nearly circular, very distinct, major axis about one and a half times into length of upper eyelid. Parotoids small, as a rule, and narrow, usually three times as long as broad, generally not touching the eye or tympanum in front. Fingers slender, first a very little longer than the second and equal to the fourth, the third the longest. Two large tubercles on the palm of the hand near the wrist with several small ones between them and the origin of the fingers. The metatarsal tubercle of the adpressed hind limb reaches the tympanum.

Tarsal fold distinct and occupying the whole length of tarsus. Toes slender but not more so than the fingers, slightly webbed at the base, the webbing not prolonged to the extremities as a narrow border. The inner metatarsal tubercle flat oval, the outer metatarsal tubercle subconical. Articular tubercles of fingers and toes simple and prominent. Head between eyes usually rough; as a rule, a distinct fold or crease in the skin across the neck from the anterior end of one parotoid to that of the other. Back, sides, and outer surfaces of the arms and legs covered with tubercles, each tubercle invariably with a horny spine coloured dark brown at the apex; a group of enlarged tubercles behind the tympanum and almost in line with the upper lip, larger than those upon the back; under-surface granular, roughest on the chest and sub-mental region.

Colour.—Pale ashy-olive, grey, light or dark brown above, with dark brown blotches and vermiculations edged with black; sides pale brown or grey with darker brown or grey spots; a light narrow vertebral stripe reaching from the occiput, or sometimes from the tip of the snout, to the vent invariably present. The posterior portion of the body covered by the thighs, when at rest, a bright scarlet or vermilion, occasionally the axillary and inguinal regions have also a scarlet patch. Throat and chest dark grey in breeding males, otherwise whitish ventrally.

Bufo carens, Smith.

This species is extremely plentiful; when out at night with a lamp one meets them at almost every step.

The habits and life-history of this species, with a description of its remarkable tadpole, have already appeared (**15**).

Bufo vertebralis albiventris, n. subsp.

A collection of eight small toads, all males, taken at Lobatsi, presented considerable difficulty in the placing of them. The table on next page is one of measurements in millimetres.

It was at first thought that they might be referable to *Bufo fenoulheti obtusum*, Hewitt (**11**), which comes from Bleskop, Rustenburg Dist., in the Western Transvaal, and not very far from Lobatsi. On comparison with specimens kindly lent by the Transvaal Museum they were found to differ from *obtusum* in the main character used by Hewitt to distinguish that subspecies from *fenoulheti*, viz. the snout character.

They were next compared with the type of *fenoulheti* kindly lent by Mr. Hewitt. The following differences therefrom are recorded: narrower interorbital space; much smoother dorsal surface; the webbing of the

Sex.	Locality.	Tympanum.	Eye.	Snout to Vent.	Between Eyes.	Eye to Nostril.	Nostril to Tip of Snout.
♂	Lobatsi	2·0	3·0	27·5	2·0	2·6	2·0
♂	,,	2·0	3·0	27·5	2·6	2·6	2·0
♂	,,	2·0	3·0	29·0	2·2	3·0	2·0
♂	,,	2·0	3·0	27·0	2·6	2·6	2·0
♂	,,	2·0	3·0	29·0	2·5	2·6	2·0
♂	,,	1·5	3·0	28·0	2·5	2·6	2·0
♂	,,	1·5	3·0	27·5	2·5	2 6	2·0
♂	,,	2·0	3·0	29·0	2·5	3·0	2·0
Averages .		1·8	3·0	28·0	2·5	2·7	2·0

toes less developed; the inner metatarsal tubercle elongated and subconical; the nostril nearer the end of the snout than the eye. In fact all the characters which Hewitt used to separate *obtusum* from *fenoulheti* are present in this form with the exception of the snout character.

During a visit to Cape Town in January the Lobatsi material was compared with the collection of *dombensis* in the South African Museum. It was found that, in the latter, the snout is considerably more blunt, the parotoids more distinct, the head broader, the metatarsal tubercles more developed, the foot longer than in the Lobatsi form.

It was also noted that the first finger is slightly longer than the second in *dombensis*; they are equal in the Lobatsi specimens.

These toads were also compared with the large collection of *vertebralis* in the M'Gregor Museum and were found to differ from this species in the same respects as *obtusum* (see Hewitt (**11**)). The occurrence of *vertebralis* at Madibi and perhaps further north seems to indicate some connection between these different forms. In a large collection from the intermediate areas they would probably be found to intergrade. The Madibi specimen preserved in the Kimberley Museum has but a few small black spots ventrally.

This Lobatsi form seems to the author to be between *vertebralis* and *fenoulheti obtusum*. He therefore places it as a subspecies of the former and names it *Bufo vertebralis albiventris*.

The writer was fortunate in being able to observe the habits and life-history of this interesting little toad. The ground colour of the adult male ranges from light grey to dark brown, covered with darker irregular markings edged with black. The upper surface of the body, at least in breeding males, arms, legs, and sides sprinkled with bright red spots which give them a pretty appearance. The under-surface white.

It is confined to the kloofs in the hills and, being strictly nocturnal, it is difficult to find except in the breeding season. During that period (end of November to, probably, end of January) the males assemble in the small, shallow pools among the rocks. The call, which is entirely different from that of *vertebralis*, resembles a hoarse *weet, weet, weet*, etc., audible at a distance of only 8 or 10 yards. The male grasps the female in the axillary region, pressing the hands well into the armpits.

The eggs are laid in strings like strings of beads and are entwined among stones, grass, or anything that may be in the water. They resemble very much those of *vertebralis* though somewhat larger; they measure 1·8 mm. in diameter and are enclosed in two gelatinous capsules, the outer of which measures 2·7 mm. when first laid, but swells to about 3·6 mm. before the larva frees itself. The eggs are black for about two-thirds of their diameter, the remaining one-third being dark greyish.

Eggs to the number of, approximately, 2000 were laid on the night of 8th December 1926. On 9th December 1926 they had hatched, the larvae measuring 3·0 mm.; they were still in the egg-capsule which had swollen to about 3·6 mm.; the tail had begun to develop; there was no sign of external gills, but the gill arches were visible; also the adhesive apparatus; invagination of nasal capsule; rudiment of ear and eye; and invagination of mouth.

On 10th December 1926 larvae had left the capsules and measured 11 mm. total length; they had large branching external gills.

On 11th December 1926 the left external gill was still long while the right had almost disappeared.

On 12th December 1926 the measurements were 12 mm. total length, tail 7 mm., the legs began to appear as tiny black buds, and from this stage on the development was rapid. The spiraculum also became visible at this stage.

On 25th December 1926 they measured 24 mm. total length, tail 15 mm. This was the greatest length reached.

On 26th December 1926 the arms, first the left through the spiraculum, came through and the tailed frogs began to leave the water almost immediately.

By noon on 27th December 1926 the tail had almost entirely disappeared; the tiny frogs measured 9 mm. from snout to vent. Thus the metamorphosis had taken nineteen days to complete as against sixteen days for *B. vertebralis*.

Tadpole (Pl. XXII, fig. 4).

Body.—Length of body about one and three-fifth times its width; nearly two-thirds the length of the tail. Eyes situated dorsally not visible from

below, the distance between them one and a half times that between the nostrils, equal to the width of the mouth.

Spiraculum.—Spiraculum fairly prominent, on the left side, directed backwards and upwards, about equidistant from either extremity of the body.

Anus.—Anal opening median, on the lower edge of the sub-caudal fin, about equal to the spiraculum.

Tail.—Tail nearly four times as long as deep, obtusely rounded at the end; upper crest slightly convex, lower one almost straight; upper crest not extending on the back; the depth of the muscular part at its base about two-thirds the total depth.

Mouth-disc (Pl. XXII, fig. 3).—Disc elliptical, the sides bordered with papillae in one row; both upper and lower edges toothed; the series of teeth is represented by the formula $\frac{2}{3}$ or $\frac{1}{\frac{1-1}{3}}$, the second upper series extending nearly as far laterally as the first, but broadly interrupted in the centre; the first lower series short and occupying the middle of the lip, the second and third uninterrupted, as a rule, and extending the full width of the disc, the third sometimes interrupted in the centre.

Colour.—Body jet-black; upper tail fin finely spotted with black; lower fin transparent save the posterior third which is minutely spotted; ventral surface transparent.

Habits.—These tadpoles lead an independent existence; they were never noticed moving in colonies. They feed mostly on the slime, etc., on the bottom and sides of their habitat.

Xenopus laevis, Daud.

This species is very common, being found in every pool. Tadpoles were also plentiful in almost every pool during the early part of December.

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EXPLANATION OF PLATES

Plate XVIII.

Fig 1. The narrow gap through which the train enters the Lobatsi basin.
Fig. 2. A view of the country around Lobatsi.

Plate XIX.

Fig. 1. Dorsal view of the female *Cinixys lobatsiana* n. sp., about [illegible] full size.
Fig. 2. Dorsal view of the male *Cinixys lobatsiana* n. sp., about [illegible] full size.

Plate XX.

Fig. 1. Side view of *Cinixys lobatsiana*, n. sp., about [illegible] full size.
Fig. 2. Ventral view of same about [illegible] full size.

Plate XXI.

Fig. 1. Dorsal view of *Bufo regularis*, Reuss., from Lobatsi, about [illegible] natural size.
Fig. 2. Dorsal view of *Bufo regularis* subsp., *gutturalis* n. subsp., from Lobatsi, about [illegible] natural size.

Plate XXII.

Fig. 1. Ventral view of *Bufo vertebralis* subsp. *albiventris* n. subsp., almost full size.
Fig. 2. Dorsal view of same, nearly life-size.
Fig. 3. Mouth-disc of the tadpole of *Bufo vertebralis albiventris*, much enlarged.
Fig. 4. The tadpole of same, about $2\frac{1}{2}$ times life-size.

Fig 1.

Fig. 2.

Photos by A. M. Duggan-Cronin. Neill & Co., Ltd.

FIG. 1.

FIG. 2.

Photos by A. M. Duggan-Cronin. Neill & Co., Ltd.

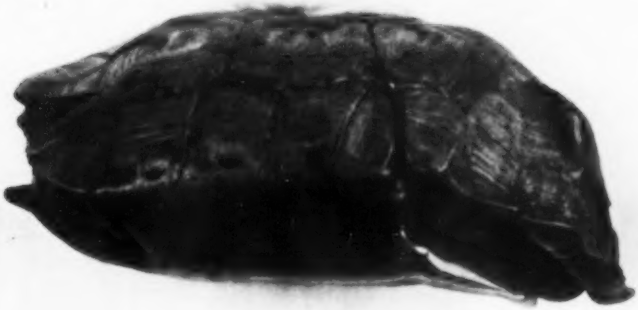


Fig. 1.

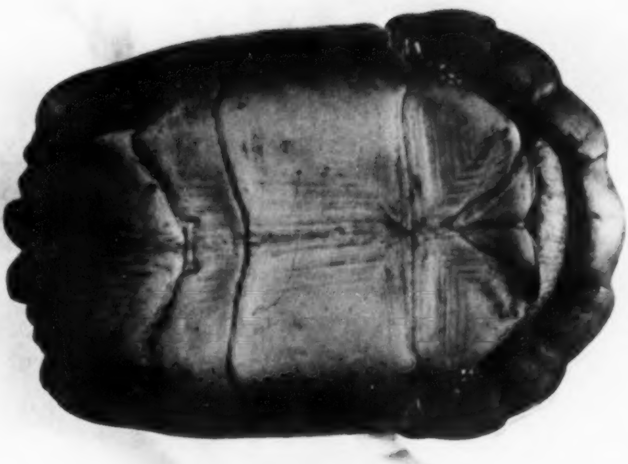


Fig. 2.

Photos by A. M. Duggan-Cronin. Neill & Co., Ltd.

Fig. 1

Fig. 2.

Photo by A. M. Duggan-Cronin. Neill & Co., Ltd.

Fig. 1.

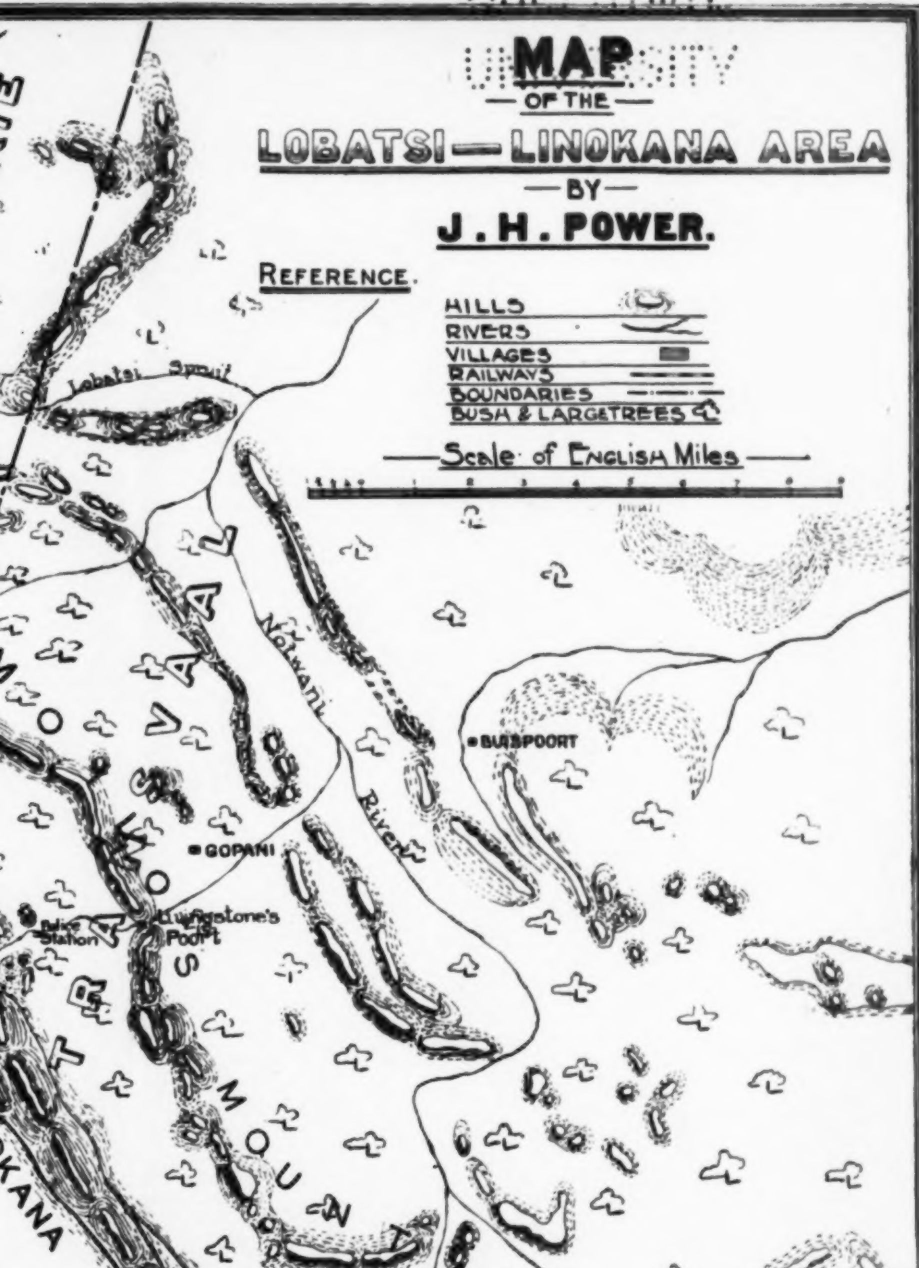
Fig. 2.

Fig. 3.

Fig. 4.

Photos by S. Tapscott. *Neill & Co., Ltd.*


PROTECTORATE
HILLS
LOBATSI
MO
BECHUANALAND
LINOKANA
WATERLESS
FLATS
Police Station


MAP
OF THE
LOBATSI — LINOKANA AREA
BY
J. H. POWER.
REFERENCE.
HILLS
RIVERS
VILLAGES
RAILWAYS
BOUNDARIES
BUSH & LARGETREES
Scale of English Miles
Lobatsi Spruit
Notwani River
BUISPOORT
GOPANI
Police Station
Livingstone's Poort
LINOKANA
HILLS

Neill & Co., Ltd.